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A REPRODUCTIVE BIOLOGY AND NATURAL HISTORY OF THE JAPANESE WHITE-EYE (*ZOSTEROPS JAPONICA JAPONICA*) IN URBAN OAHU

Sandra J. Guest

Department of Zoology
University of Hawaii
Honolulu, Hawaii

ISLAND ECOSYSTEMS IRP

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Abstract

The White-eye (Zosterops japonica japonica) is a small passerine bird, first introduced to Hawaii from Japan in 1929. Since that time it has spread to all of the main islands, and now is found from sea level to tree line and is probably the most abundant bird in Hawaii. This study considered the breeding biology of the population of White-eyes (about 100 birds) on the University of Hawaii Manoa campus (about 84 acres). It began in late 1971 and extended through the summer of 1973.

The breeding season begins early in the year (the first nests in late February), continues through July, and ends with an annual molt in August. Initial pairing of juveniles probably occurs in winter flocks and the birds then remain together for at least more than one season, possibly for life. Each pair occupies a territory averaging 1.6 acres, the size being related to the vegetation present. Territory is defended by singing of the male, but both male and female may take active roles in chasing other singing White-eyes from the territory; however, trespassing of foraging White-eyes is generally permitted.

Nest location is related to environmental factors (i.e., wind direction), but the plant species in which the nests are constructed is extremely variable. Both male and female construct the nest (a neatly woven cup usually suspended in the fork of a small branch). Average clutch size is 3.14 eggs (range 2 to 5 eggs), incubation period about 11 days, nestling period 9 to 10 days, and fledgling period about 20 days. Three successful broods are possible per pair in one season. Both parents incubate, carry food to the young, remove fecal sacs, and defend the young.

The success rate, from egg to fledging, is 58.6%; this is very high for a small, altricial, tropical bird. Weather and wind are the most important factors in the mortality of nests. The overall success of the species in Hawaii is discussed in terms of the positive and negative factors in the breeding biology. Diet and social behavior of adults are discussed also.

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A Reproductive Biology and Natural History of the Japanese White-eye (*Zosterops japonica japonica*) in Urban Oahu

The White-eye in Hawaii

Since the introduction of the Japanese White-eye (*Zosterops japonica japonica*) to Hawaii in 1929, it has spread to all of the main islands and become the most abundant bird on the main Hawaiian Islands. My study of this species began in late 1971 on the University of Hawaii Manoa campus and has extended to the summer of 1973. Very little had been done on the White-eye in Hawaii, and this project was undertaken to outline the general breeding biology and life history of the species in a lowland residential area.

Delacour and Mayr (1946) describe *Z.j. japonica* as "Citrine green above, more yellow on forehead. Broad white eye-ring. Throat and under tail-coverts pale yellow; breast, abdomen, and flanks dirty white. Iris brown." The range of the species is the "main islands of Japan from Honshu to Kyushu and islands between Japan and Korea" (Mayr, 1967). It was introduced to the Hawaiian Islands in 1929 by the Board of Agriculture and Forestry, according to Caum (1933).

There were later introductions by Hui Manu and private individuals, and the White-eye was established on Oahu and possibly Kauai by 1933 (Caum, 1933). By 1960, Richardson and Bowles (1964) felt that it was the most abundant bird on Kauai, but White-eyes were in reduced numbers in the highest areas of virgin forest. In 1937, 252 birds were introduced to the big island of Hawaii to help eradicate insects (Hilo Tribune Herald, 1949). The species is now present on all of the main islands, and is probably the most common species. Berger (1972) states "The White-eye is an example *par excellence* of the success of an exotic bird released in a foreign environment. ... it is found both in the very dry and the very wet habitats; and it is found from sea level to tree line on the mountains of Maui and Hawaii."

This phenomenal success is not suprising, in that White-eyes have been successful on other oceanic islands. Zosteropidae have, in fact, colonized more oceanic islands than any other passerine family (Moreau, 1964). In 1956, Betts discussed some of the reasons for this success on islands. The birds tend to flock in the winter season, so there is a greater chance that several will arrive if blown to an island. Besides being comparatively omnivorous "they are sedentary and, in consequence, having arrived at an island where they can exist, are content to remain there." Gill (1971) refers to White-eyes as "opportunistic generalists" that "thrive in disturbed environments and ... island situations."

Although they were introduced to Hawaii by man, White-eyes are very adept at colonizing islands on their own. In New Zealand, Z. halmaturina crossed 1200 miles of water from Australia, became established, and is now common (Wilkinson, 1931). Ely (1971) reported sightings of White-eyes between Oahu and Johnson Atoll, and feels that it is possible that they might reach and colonize the Marshall Islands or Line Islands.

It has been suggested that the success and rapid increase of White-eyes is related to the decrease of native birds (Dunmire, 1962), but this has not been shown to be true. They don't appear to compete for nesting sites with the honeycreepers and there is not enough evidence to say if they compete for food (Berger, 1972). However, they do feed with the honeycreepers in the native forests. What parasites may have been transmitted to endemic birds by way of the White-eyes is unknown. The White-eye is known to become infected with malaria (Navvab Gojrati, 1970). I have found infections of coccidia and nematodes in several individuals. Furthermore, it may be worthwhile to note that Lack (1971) speculated a "factor in the reduction in the numbers of species is the tendency on small or remote islands for one species with a broader niche to replace two more specialized species."

The White-eye Elsewhere

According to Moreau (1957), "the Zosteropidae (White-eyes) are a tropical passerine family, with a range over the whole of the Ethiopian Region and eastwards, through the islands of the Indian Ocean and India to Japan, the central Pacific and Australasia. ... The family is for the most part very homogeneous, ... presenting special difficulties for the taxonomist. ... Birds usually assigned to the genus Zosterops comprise more than four-fifths of the Zosteropidae." Nearly all members are under 140 mm in length. White-eyes are typically green (ranging from grey-green to bright yellow-green) dorsally and yellow and white ventrally, with a conspicous eye-ring. There are nine functional primaries and 12 tail feathers, and the sexes are alike.

At one time the White-eyes were placed in the Paridae, Dicaeidae, and Meliphagidae. Of Oriental origin and closely related to the Nectariniidae and Didaeidae, they probably evolved from the Old-world warblers (Sylviidae; Fisher and Peterson, 1964; Skead, 1967).

Within the family there is some taxonomic confusion. In many groups of birds coloration has been used as a safe criterion of species, but unfortunately color difference apparently has little taxonomic significance in Zosterops, and there are many examples of incorrect classification (Hall and Moreau, 1970). Two African species (Z. virens and Z. atmorii), once seperated on the basis of plumage color, are probably one species. They interbreed freely (Skead and Ranger, 1958). In New South Wales, Chisholm (1932) found great similiarities in size, shape, structure, nest building, egg color, and general habits of Z. lateralis and Z. halmaturina. Only the plumage color varies. On the basis of body dimensions, four former African species have been reduced to two species (Clancey, 1967; Moreau, 1957). And within one species in New Zealand (Z. lateralis), Marples (1945) was able to seperate nine categories on the basis of belly color.

Skead (1967) explains this confusion in color variation by discussing the two groups of pigments involved: carotenoid and melanin. Both types are found in each feather in varying proportions. Abrasion, type of melanization, and humidity seem to affect the final appearance of color. Furthermore, it has been reported that at least one species of White-eye (Z. japonica) becomes darker when in captivity (Ingram, 1908). This is also true of other species of birds (Bent, 1968). Whatever the reason, color variation has caused a great deal of confusion in classification of the 200 forms of the Zosteropidae; only 80 species are now recognized.

The taxonomy of this group is still far from being worked out completely. Even the more recent works, which are based on body dimensions instead of plumage color, may be misleading, and behavior and ecology should be studied before final taxonomic decisions are made. Harrison (1968) has shown that two morphologically similiar species in western Australia (Z. lateralis and Z. lutea) are ecologically very divergent. All of this points to the fact that more work is needed on the Zosteropidae of the world.

Materials and Methods

For the most part, this paper is based on field observations. However, there were certain techniques which were employed to collect data. These are outlined.

Banding

All birds banded on campus were banded with a U.S. Fish and Wildlife metal band and two or three plastic bands in different color combinations, so each bird could be recognized as an individual. I used a mist net to capture the birds (see Low, 1957). For White-eyes, the best method is to place the net low to the ground, in front of a bush for camouflage. I used two techniques to net birds.

The first technique requires studying the flight paths of birds in one area, near a feeding or bathing location where large numbers of birds congregate, and then placing the net across one of the paths. I did not leave the net unattended, and removed the birds immediately.

A second technique is to trap the parent birds at their nests. A nestling or fledgling is placed on the ground, behind the net. The parents then swoop over the chick, and into the net. If the adults are hesitant, the chick may be dropped to the ground, and as it flutters down, the adults will fly with it into the net (see page 64). A variation of this technique that is very successful, is to place an adult in a cage behind the net. Other White-eyes will become curious and fly into the net.

I also banded young birds in the nest, or on the day of fledging. It is best to band them on the eighth day after hatching, or on the day of fledging. If older than eight days, they will leave the nest prematurely, and if older than 10 or 11 days, they become rather difficult to catch.

Birds were sexed by behavorial differences later in field observations. I recorded weights of some birds, molt, and general condition of bird at time of banding. No attempt was made to recapture individuals, but a record was kept of further sightings.

A funnel trap as described by Cunningham (1946b) was used, but it was unsuccessful.

Determination of Territory and Population

There are various references to mapping territorial boundaries, but many seemed unsuited for White-eyes because aggression is often seen in the field but not at well defined boundaries between territories. This also is true of other species of Zosterops (Flemming, 1942). I did not see actual boundary defense in enough instances to successfully map even one territory completely. Also it is difficult to identify individuals, even when banded, because the birds are very active and move rapidly in the foilage. For this reason a technique such as described by Odum and Kuenzler (1955), where individuals are identified in different parts of their territory and the lines of boundary drawn according to where the bird spends the majority of time, is not applicaple. However, the males do sing for a period of 20 to 40 minutes at sunrise, and I used this to determine territory.

The approximate territory boundaries were measured by finding the song positions of the males during the early morning singing. This was done early in the season to eliminate the chance that juveniles might be singing. I then divided the area evenly between the song positions. Since the song positions change during the season, a later mapping would show slightly different territories.

I feel that this is a fairly accurate technique in that, where territory defense was observed, it corresponded roughly to the boundary lines, and the lines tended to fall along natural boundaries (i.e., tall buildings, open areas).

Each territory was ranked by size. Size was determined by cutting out a figure of the territories from a map and weighing the paper. Forty-two territories had all four boundaries mapped, and every fourth one was examined for the vegetation present. The vegetated area was then compared to territory size. The total population (resident) was estimated by assuming a pair of birds for each territory.

Song

To study the singing cycle, a transect of about 9266 meters was laid out across campus. I walked it at an even pace (total time about 30 minutes), at various times of the day and noted the number of songs heard. From this information, I determined the relative amount of singing at different times of day.

Any time a song was heard during the season it was also noted, and this was compared to the stage of the nesting cycle of the singing bird. This yielded a rough estimate of when singing occurs during the individual cycle.

The Nest

Certain measurements were taken at the nest. Height was measured from the bottom of the nest to the ground directly below the nest, with a tape measure. In certain instances, I measured height as the distance from the bottom of a nest to the roof of a building. Distance from the edge of the nest to the end of the nest limb, the distance from the nest to the base of the tree, cup depth, cup diameter, rim thickness, bottom thickness, and diameter of branch where nest is attached were also measured (see fig. 1). As a rule these were measured in milimeters, to the nearest 0.1 mm.

Several nests were collected and placed in a Tüllgren funnel, and the fauna preserved in 70% alcohol. Lice and insects were mounted in Hoyers Solution and incubated at 40°C. for two weeks.

I recorded whether the nests were on the leeward or windward side of the tree. Interspecific and intraspecific spacing of nests was measured by marking the nests on a map and measuring distance, or was determined directly with a tape measure in the field.

The Egg

Eggs were weighed on consecutive days during the 1972 season at several nests. Air cell diameter was measured on consecutive days(fig. 2). Clutch sizes were noted.

Measurements included the longest and widest dimensions of the egg measured to the nearest 0.1 mm, and the long diameter of the air cell to the nearest 0.1 mm, with calipers. Weights were taken at the nest with Pesola scales (accurate to 0.1 gms). Color was recorded. See Figure 2 for more detail.

Measurements of Young and Adults

Several measures were taken on developing birds. They were weighed on consecutive days with Pesola scales, to the nearest 0.1 gms. For information on feather tract development, pictures and sketches were made at the nest.

Measurements of adult birds (culmen length, tarsus length, wing and tail lengths) all are as described by Pettingill (1970).

Aviary techniques

I maintained an aviary of 8 ft. x 6 ft. x 4 ft. for 18 months. Adults were fed honey-water and vitamins, cereal, oranges, apples, and one soft fruit every day (see Eddinger, 1969). Fruit was usually hung in the cage, rather than crushed in dishes.

Several birds were hand raised, and cereal, vitamins, egg yolk, fruit, and honey comprised the main diet. The young were fed every 10 minutes at fledging, or when they called for food.

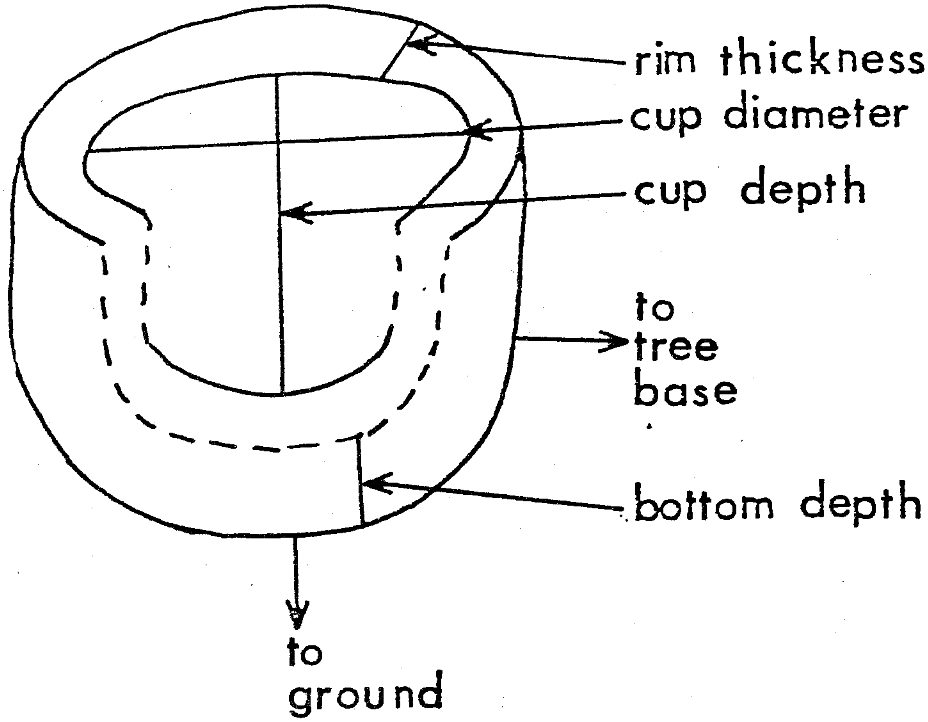


Figure 1. Measurements of the Nest.

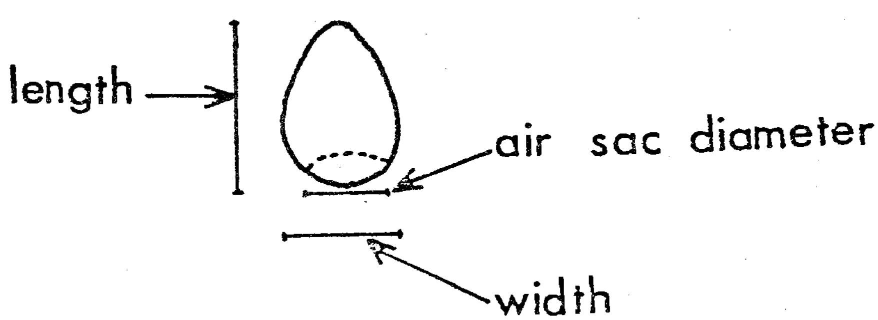


Figure 2. Measurements of the Egg.

Results and Discussion

Population and Study Area

The study population is located on the University of Hawaii Manoa campus. It is an open area, with a large number of cultivated trees and shrubs, and is somewhat similiar to a residential area. The main campus covers 83.5 acres, and includes approximately 52 breeding pairs of White-eyes. This gives an average of 0.62 pair per acre, and a density of 124 birds per 100 acres. Kikkawa (1962) found _Z. lateralis_ to have a density of 1.2 pair per acre in a wooded area in New Zealand.

General Seasonal Cycle

Breeding seasons may be initiated by various factors (food supply, preciptation, increase or decrease of day length; Van Tyne and Berger, 1971). In tropical areas the problem of determining what initiates the season is complex, and several factors may be involved. In Hawaii, the nesting or breeding season starts in January or February, and this corresponds to the wettest period of the year (Blumenstock and Price, 1972). This suggests that there may be a correlation between rainfall and initiation of the breeding season.

There is one report that the breeding season of White-eyes in Hawaii extends from February through November (Ord, 1971), but he stated (personal communication) in June of 1973 that he did not feel the normal breeding season was that long. In both 1972 and 1973, I found the earliest sign of nesting in January and the first nest with an egg in February. The season extends to July. Since the raising of a complete brood takes about 50 days, a single pair may raise as many as three successful broods in one season. In 1972, at least two pairs completed three successful broods.

An annual molt begins in late July or early August, but one bird was found molting during the summer. Two molts are present in Z. lateralis in New Zealand (Marples, 1945), so a second molt in Z. j. japonica is possible.

Flocks are common during the nonbreeding season. Large flocks (I saw one of over 100 birds at Diamond Head during the summer of 1972) may be composed mainly of juveniles. My reason for this statement is that several known banded pairs were seen in small flocks near their territory throughout the summer of 1972. One pair was never seen with more than eight to ten birds, and always together within the small flocks (observed more than ten times). Winter flocks begin to form in July and begin to disintegrate in January and February, when territory establishment and defense begins. This pattern is similiar to other species of White-eyes (Cunningham, 1946a; Marples, 1944).

In comparing the 1972 and 1973 season, the 1973 season was about two weeks later than the previous season. I have some evidence suggesting that in 1973 there may have been less food available. My evidence for this is based on some observations of inch worms (Lepidoptera, Geometridae), a very common food of the White-eye. In 1972, while searching for nests I had occassion to move through very thick Haole Koa (Leucaena leucocephala). After emerging from the vegetation I could easily pick 10 to 15 larvae out of my hair and off my clothing. In 1973, I walked through the same stand of Haole Koa, and spent about the same amount of time in the field, and did not find more than one inch worm at a time on my body. This suggests that the food may have been less abundant, and might explain the later start to the 1973 season. There was a very severe winter drought in 1972-1973 that could have affected the abundance of food. Skutch (1950) found that in Central America the period of greatest food abundance correlated with the time when 80% of the species nested (Van Tyne and Berger, 1971), so the abundance of food availability may influence the start of the season.

Table 1

Calendar for 1972-1973

Flocking, breeding season, and molt are indicated by solid and broken lines in the left column.

Flocking

Breeding Season 1972

Flocking

Molt

1971	
Dec. 5	Beak clapping and chasing in a flock of 4-6 birds, lasting about 10 minutes.
1972	
Jan. 25	Flock of 7-10 birds resting, preening, and allopreening in a Banyan about mid-day. Some of the birds in pairs within the group.
Feb. 3	Birds flying to and from a feeding area in pairs, joining flock at the fruiting tree.
Feb. 10	Flock of 8-10 birds feeding, late afternoon.
Feb. 15	Bird carrying nesting material at Diamond Head.
Feb. 19	At Diamond Head several White-eyes wing fluttering and chasing in a Kiawe tree.
Feb. 20	First egg of the season (estimate, as nest was found during incubation period).
Feb. 21	Aggression and beak clapping at food trees seems more intense. Birds still feeding in groups of three or four.
Feb. 22	Bird carrying nesting material to a site, but nest was never completed.
March 14	First fledgling of the year.
April-May	Birds not in flocks of more than three or four (family groups).
May 10	Largest number of active nests, during the 1972 season.
June 24	Last complete nest started.
July 20	Last incomplete nest started.
July 25	Last fledgling of the year.
July 29	First bird in molt.
Sept. 1	Last bird in molt.

Flocking	October	A bird on territory, singing, where it had not been during the previous season.
	November	Numerous sightings of birds in small flocks.
	Dec. 14	Bird carrying nesting material, but no nest was started.
	1973	
Breeding Season 1973	Jan. 20	Bird carrying nesting material, but did not start nest.
	Feb. 18	Nest started, but never completed.
	Feb. 26	Several birds chasing and beak clapping in a Fiddlewood tree.
	March 1	First egg of the season.
	March 4	Singing extremely common all across campus.
	March 11	First fledgling of the year.
	May 15	Largest number of active nests for 1973 season.
Flocking	June 26	Flock of more than 8 birds feeding in a Monkeypod tree.
	July 12	Last complete nest started.
	July 20	Last egg of the season laid.
	August 11	Last fledgling of the year.

Sound Production

White-eyes have a variety of vocal sounds. Some species are capable mimics (Chisholm, 1932), and the White-eye in Hawaii has been known to mimic another species (Guest, 1973). In Japan, the White-eye is a favorite cage bird, known for its singing ability (Munrc, 1960). Following is an outline of their repertoire.

A. Nonvocal sounds

1. Beak clapping--used in conjunction with displays; a component of aggression.

B. Vocal sounds

1. Call notes

a. location notes--'tseet', given when in a flock, or when feeding in pairs, by male and female.

b. fledgling notes--very similiar to location notes, given by fledglings when hungry.

2. Chitter--a harsh scolding noise uttered when the birds are upset or disturbed, by both male and female.

3. Whine--similiar to and sometimes preceeding the chitter, given in conjunction with aggressive displays, by male and female.

4. Songs

a. whisper song--a rambling warble given in quiescent periods that is so quiet it can not be heard more than about three meters away; seldom heard in the field.

b. 'flight song'--a series of stretched-out call notes given when the birds take to the air, usually lasting only a few seconds.

c. primary (territory)song--a loud warbling song, given by only the male. It is sung from a prominent position within the territory, and has the function of defining the territory. One singing bout may include from one to 50 songs, each song averaging about five seconds and the period between songs, averaging two or three seconds.

I have heard the primary song of the male in every month of the year, but there is an increase of singing during the breeding season. Superimposed on this yearly cycle is a daily cycle correlated with the nesting cycle (see figs 2 and 3).

The daily cycle begins with a period of song about 20 to 40 minutes in length at sunrise. There is a sharp decrease in frequency of singing during the rest of the day. The slight increase in the evening shown on Figure 3 is not significant (one-sided t-test). I determined these frequencies from transect walks on five different days early in the 1973 season. Mees (1957) reported dawn and evening song in Z. japonica.

The nesting cycle of individual pairs is synchronized with a song cycle such that song increases during the nest building, incubation, and fledgling period and decreases during the nestling period. The decrease of singing during the nestling period may not be explained by the fact that the male feeds the young and might become very busy carrying food and have less time to sing. Feeding rate increases to a maximum during the early fledgling period also.

Figure 4 shows the individual song cycles in relation to the nesting period. These data were collected from five pairs that were each observed through at least one cycle. One pair nested outside my office and I was able to hear their song from inside the building and therefore make almost continous observation on them.

A main function of song in the White-eye is territory defense, and if a male attempts to sing in a territory other than his own, he is chased away by both the male and female occupying the territory. Such an incident is related in the following account from my field notes.

March 19, 1973--Nest 9-73 in second day of incubation. The female from this nest is banded.

1245--Male releived female at nest and began to incubate. Female flew into bushes about 10 meters from the nest.

1306--Male very alert on the nest.

1307--Female feeding in Haole Koa about 12 meters from nest. An unbanded bird began to sing from a Kukui tree about seven meters from the nest and well within the banded pairs territory. I had never heard song from this tree. The banded female began to chitter loudly, and wing flip from the area where she was feeding. Male left nest and flew to female, and both then flew to Kukui tree and chased the intruding bird. A fourth unbanded bird joined the group in the Kukui, and for the next several minutes I could not identify any of the individuals involved. Chasing, wing quivering, and wing flipping, beak clapping, and chittering ensued. Two birds flew away and male approached the nest and fluffed his feathers.

1316--Female joined male in bushes near nest. I lost sight of both of them in the foliage.

1326--One of the pair approached the nest and began to incubate.

Another function of song in White-eyes is probably that of social stimulation, and will be discussed more fully in the section on territorial behavior.

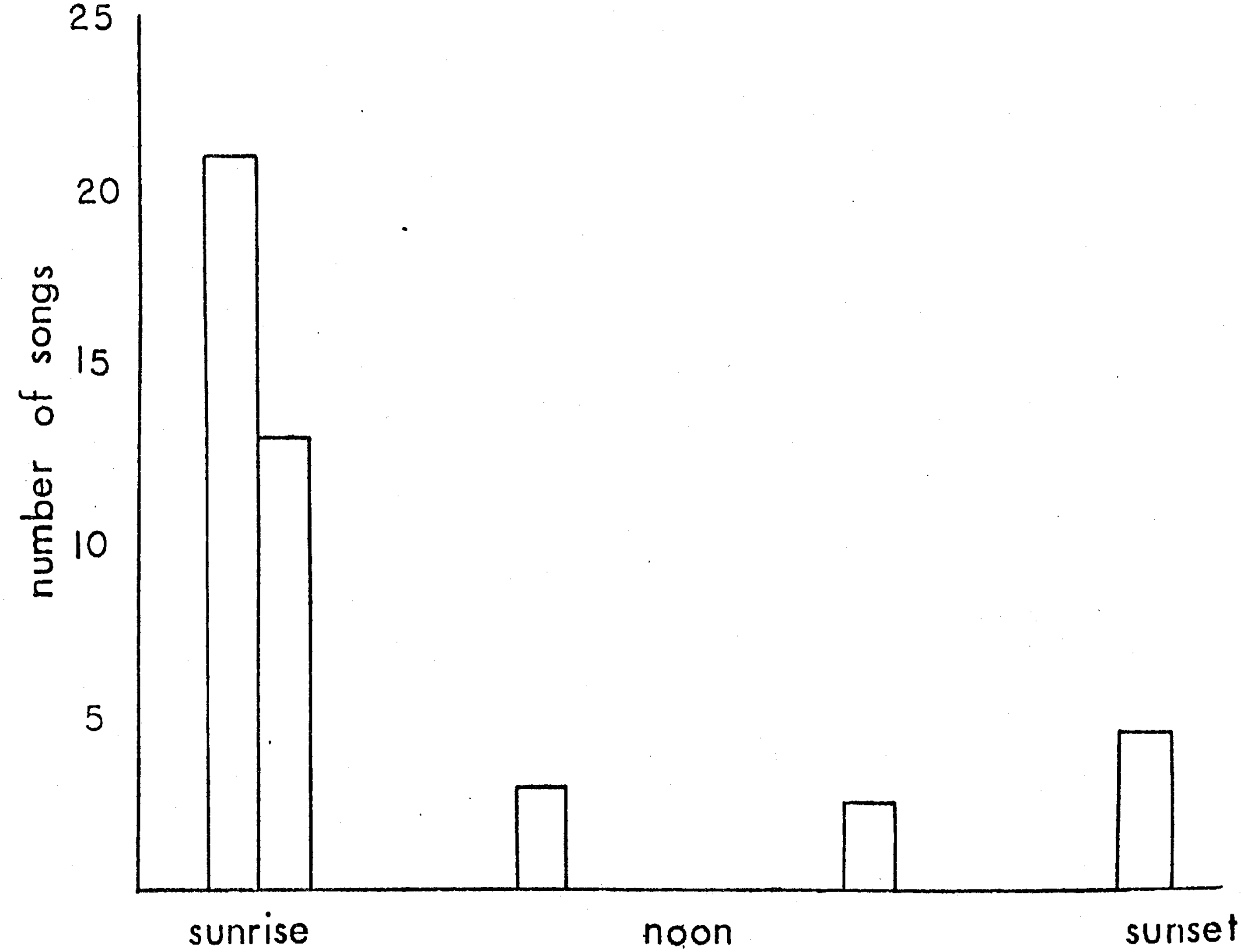


Figure 3. Daily Song Cycle.
The number of songs represents mean number heard during one transect walk (30 minutes), at four different times of day. The data are from five days, March-May 1973.

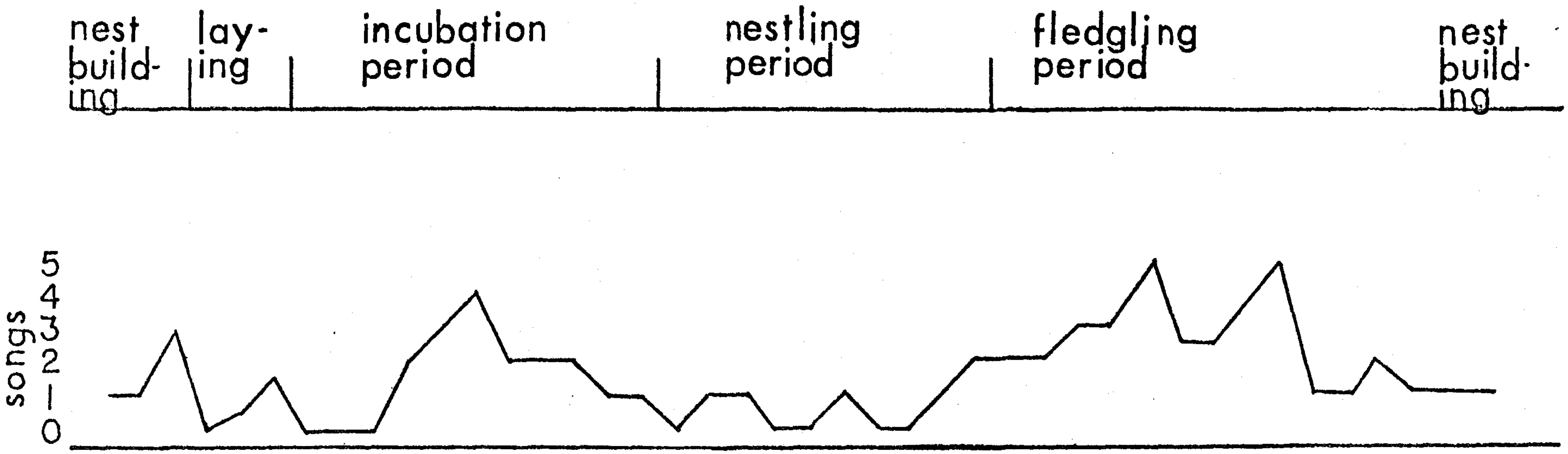


Figure 4. Singing in Relation to Individual Nesting Cycle. Data are from five pair that were observed through at least one cycle (1973). See text for further discussion.

Territorial Behavior

Territory is defined as any defended area (Hinde, 1956). There have been many discussions in the literature of territory function in birds (Hinde, 1956; Nice, 1941). Not all of the functions discussed apply to White-eyes in Hawaii, and there are probably several functions that this behavior does fulfill.

The White-eyes on campus are spaced such that each pair has an average of 1.6 acres (range of 45 pairs is 0.31 acres to 3.40 acres; one territory measured 6.3 acres but it was abandoned in March before breeding occurred in 1973). Territory size may fluctuate slightly as the season progresses. At one location on campus a building was being constructed during the beginning of the 1973 season and several trees were removed. All of the birds seemed to shift out of the area to adjacent territories, but their relative positions remained constant. Another example of territory fluctuation occurred in a group of large banyans, with a very dense population of singing males (about three pairs per acre) in 1972 and 1973. During the season of both years, at least one pair (different pairs in 1972 and 1973) moved to adjacent areas to build after unsuccessful nesting attempts. For the most part, however, white-eye territories are stable throughout the season. Figure 5 diagrams the territories as they were in April of 1973.

From one season to the next individual birds may shift to new territories, but usually remain in the same general area. Of ten pairs banded on campus in 1972, four nested on the same territory, one pair moved to a new territory about ¼ mile from their 1972 territory, one moved to an adjacent territory, and four pairs were not seen, in 1973.

The availability of food has been suggested as being important in determining territory size in some birds. However, White-eyes feed not only on their own territory, but on adjacent ones. At every nest observed for any regular period of time, I observed the adults fly out of the territory and return with food to feed the young. Other foraging White-eyes are not chased out of the area, but permitted to forage throughout. I have observed foraging White-eyes as close as two meters from an active White-eye nest, without being chased (observed at three different nests). Large numbers congregate at feeding areas (i.e., fruiting trees) year around, regardless of territory.

Tinbergen (1957) suggests that food can be a limiting factor even when mutual trespassing is involved. Ideally, each territory would support the same relative number of birds. Beer, Frenzel, and Hanson (1956) feel that there are a number of factors besides food availability important in minimum space requirements for nesting passerine birds. The most tenable explanation is that "territory offers protection from interference in the orderly sequence of the nesting cycle."

I feel an important function of territorial behavior in the White-eye is the familiarity of the area which the bird gains. As evidence for this, I have observed a banded bird gathering nesting material on it's 1972 territory, and carry it to the 1973 territory to construct the nest. This pair spent a great deal of time "trespassing" and feeding on its 1972 territory. The two areas were adjacent.

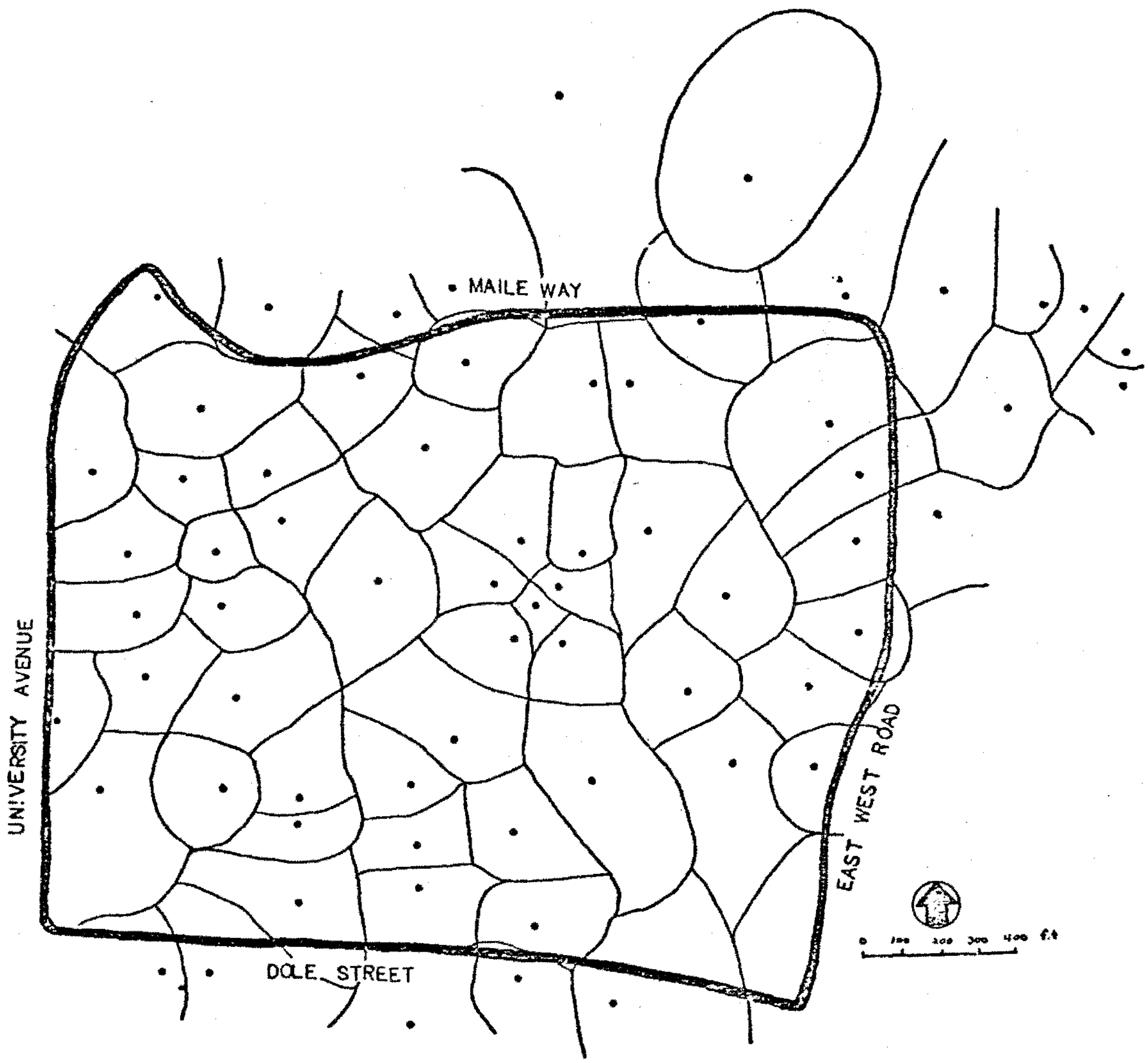
The spacing of birds on campus is related to vegetation. By ranking all the territories according to size, and examining every fourth one in terms of percentage of area covered by vegetation, I found the percent of area covered by vegetation increased as territory size decreased (see fig. 6). Kikkawa (1962) found a higher number of Z.

lateralis per acre in a wooded area than I found on campus (the comparison may mean little as these are different species). Furthermore, other factors than vegetation density are probably important in determining the final density because Richardson and Bowles (1964) reported White-eyes to be in reduced numbers in the rain forests where the vegetation density is high. Never-the-less, this system of dividing the area in terms of vegetation density, allows an efficient use of the available area for breeding.

Tompa (1962) found that, in certain cases, territory could limit the upper bounds of population density in Song Sparrows (Melospiza melodia). Brown (1964) discussed territoriality as a population control in birds and reached the conclusion that it probably has not evolved as the major factor of population control in that even though an entire population might benefit, the "changes in gene frequency are the result of competitive advantages accruing to individual geneotypes rather than to the group as a whole." I feel that although territory is surely related to the population density, there are other functions that this behavior fulfills in White-eyes.

Another function that is attributed to territorial behavior is that of social stimulation. Darling (1952) suggests that "one of the important functions of territory in breeding birds is the provision of periphery--periphery being defined as that kind of edge where there is another bird of the same species occupying a territory. ... The breeding territory has little to do with a sufficiency of feeding ground for raising the brood. It is a focal point or two--the nest site and the singing post-- and periphery." Territorial behavior is a social phenomenon, and it has survival value." That territory in the White-eye has such a function, I have little doubt. Song (territory defense) was seldom heard from one male without being answered by another. Furthermore, song increased as the birds came into breeding condition at the beginning of the season. That such stimuli can affect the behavior of birds has been shown by Lehrman (1964). White-eyes usually sing from prominant positions where they can be seen by adjacent singing males, providing further stimuli. Also, the one pair that occupied the largest territory (6.3 acres) abandoned it before breeding. This suggests that they may have "prefered" to be in an area of higher density of birds, and more social stimulation.

The two song cycles superimposed on the reporductive cycle may also be explained in terms of increasing the social stimulation. During the first few minutes of the day the presence of other breeding males is reinforced for each pair. A song increase during the fledgling period could serve two functions, that of making the parents (male) more conspicous than the young and in bringing the pair back into condition to renest. A second nest is built immediately after the young become independent, if not started while they are still being fed by the adults.



RELATIVE SONG POSITION AND
APPROXIMATE TERRITORY SIZE
APRIL 1973

Figure 5.

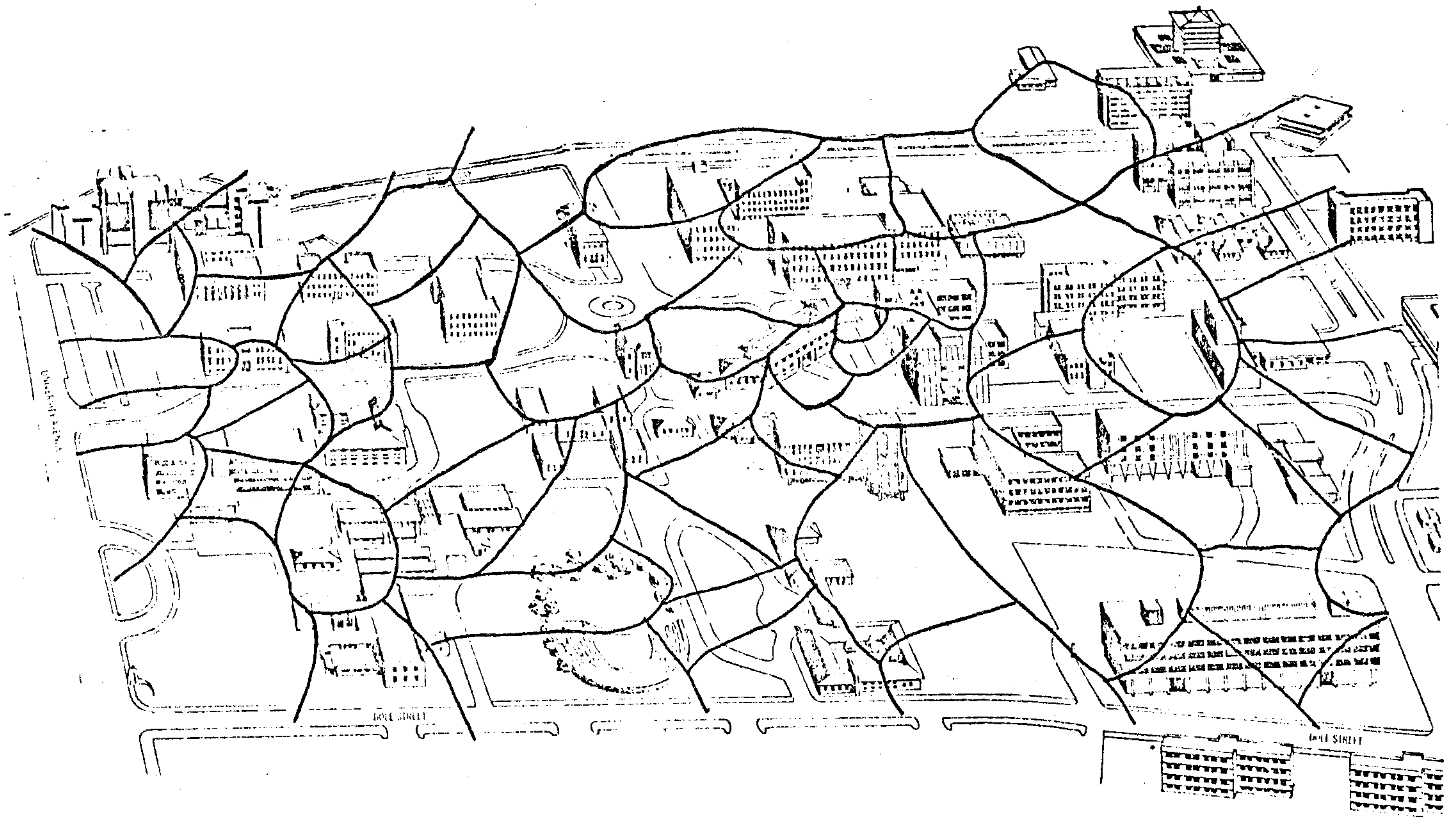


Figure 5a. Territory in Relation to Buildings.
This map is not to scale. For accurate representation, see Figure 5.

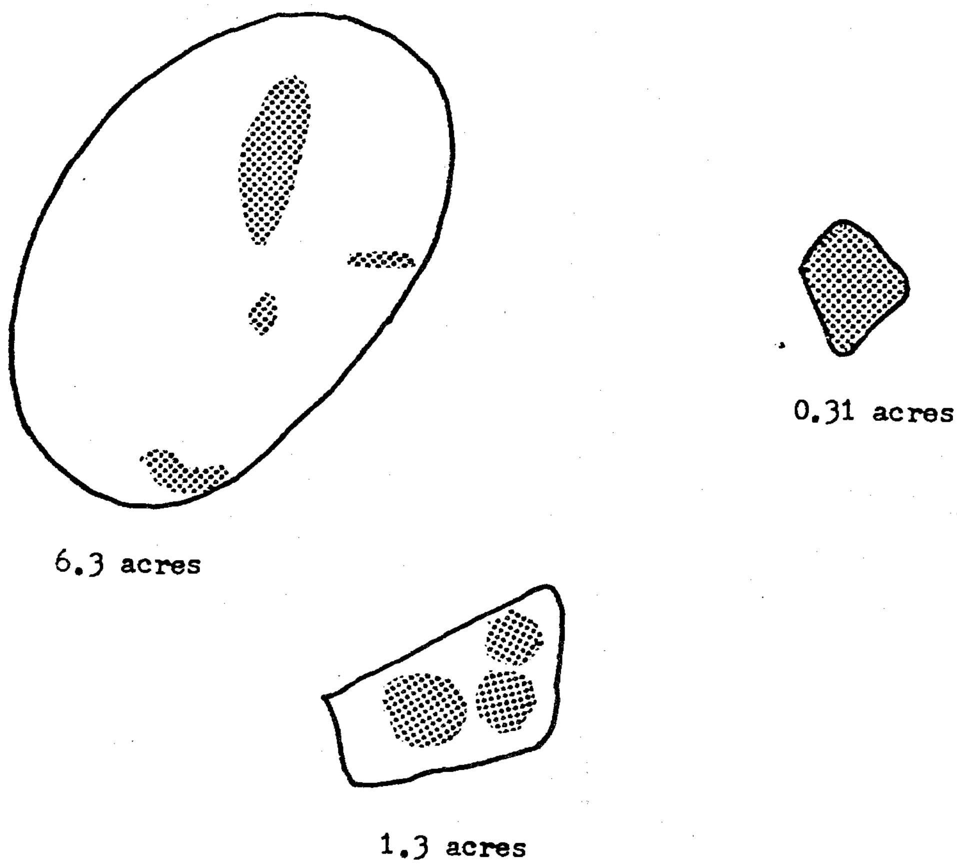


Figure 6. Territory Size in Relation to Vegetation. These diagrams represent three territories, ranging in size from the largest on campus to the smallest. The stipled area represents that area covered by vegetation (trees, shrubs). The largest territory (6.3 acres) was abandoned before nesting occurred. Measurements were taken in 1973.

Courtship, Copulation, and Nest Site Selection

Kunkel (1962) describes pair formation in Z. palpebrosa from aviary observations. "During pair formation the male offers his head to the female for preening, thus suppressing, at least partly, her tendencies to attack or to flee. ...vibrating the wings is preformed during pair formation and before nest building. The female also vibrates the wings when soliciting for copulation." I have observed, in three wild banded pairs, one bird following the other through the foliage, the bird behind wing quivering. And in one case the female was following and wing quivering, and in one case the male; the sex was not determined for the third. This behavior was not followed by copulation, and occurred at the beginning of the nesting cycle, just before nest building in all three cases. Initial pair formation probably occurs in the winter flocks, and the birds remain with their mate at least two seasons.

Copulation has been observed on three seperate occassions. In one case it occurred about five meters from the nest, three days before the first egg. There was no precopulatory display. The male mounted the female six times. Both then hopped to a nearby branch and engaged in allopreening (mutual preening). The sequence was similiar in the other two instances.

Because the birds stay together for longer than one season, there may be no need for elaborate courtship to bring the sexes together. Pair bond maintanence would be of most importance. Allopreening is very common between mates, and Harrison (1965) suggests that one of the main functions of allopreening is to strengthen the pair bond. Kunkel (1962) describes feeding of the female by the male in Z. palpebrosa, when she threatens him, but I did not observe any feeding between adult birds.

Nest site selection was observed at one nest, but the birds were unbanded so I don't know which was the female or male. One bird flew to a branch in a Monkeypod tree. It gave a variation of the 'tseet' call note that I have not heard before or since. The other bird flew to the spot immediately from an adjacent tree. They engaged in allopreening. Nest construction began the same day.

The Nest

White-eyes have "semipendent cuplike" nests (Van Tyne and Berger, 1971), regular in size, shape, and construction, with the nesting material varying slightly from nest to nest. Both sexes build, dividing the work evenly. The period necessary for completion varies with the time of season and stage of breeding cycle. A new nest is constructed for each brood.

Nest measurements for 1972 and 1973 are summarized in Table 2. Cup diameter and depth vary slightly from nest to nest, while bottom thickness and rim thickness deviate more. Nests are generally very regular in shape and construction, but I found several that were extremely unusual. One nest had a rim thickness of 10 mm on one side and 61 mm on the opposite side. It was very secure, despite the irregular shape. Branches where the nests are attached (nests are usually attached on at least two sides and sometimes almost all the way around the cup) I found to never exceed 13 mm, averaging about 6.6 mm. There was no difference in the nest measurements of 1972 and 1973 (t-test).

Table 2

Nest Measurements (in mm)*

	Cup Diameter	Cup Depth	Bottom Thickness	Rim Thickness	Diameter of Branch where Nest is attached
Mean	56.23	41.73	18.45	11.62	6.61
Standard Deviation	6.30	7.34	11.80	8.42	6.25
Number	18	15	10	12	15

* No significant difference between 1972 and 1973 measurements (t-test).

Nest material includes a variety of things (grass, fine plant material, string, tin foil, plastic, hair, spider web, spider cocoons, leaves, mosses, etc.). The cup of the nest is composed of fine grass woven together with spider web. The most common type of grass is *Eragrostis tenella*. On the outside, colored string, plastic, paper, cocoons, or miscellaneous material is common. Cocoons are reported in the literature for other species of *Zosterops*. I found the cocoons used by the birds to be from the spider family Araneidae.

In 1906, Dove stated that White-eyes probably wipe the empty cocoons on the nest after feeding the young; however, I found the birds carrying cocoons to the nest before incubation began, and never saw them being carried to the nest to feed the young. (I have seen once, adults feeding fledglings spider cocoons.) Furthermore, many nests had no cocoons, but invariably they had some colored material or white paper on the outside. I feel that the white cocoons and colored material probably serve to break the outline of the nest and thereby camouflage it. The nest becomes more difficult to see giving this behavior survival value.

The nest lining is very fine material, commonly human hair. In two cases, I found the young birds tangled in this fine material, so they were unable to fledge from the nest. Instead they dangled from the nest. I did not find them until they were dead, so I don't know the adult behavior.

Nest material is not collected entirely on a birds territory. A very common habit is the stealing of nest material from active nests of other birds. I have observed White-eyes stealing material from active House Sparrow (*Passer domesticus*) and Linnet (*Carpodacus* mexicanus frontalis) nests. Frings (1968) reports that White-eyes steal nesting material from the nests of the 'Elepaio (Chasiempis sandwichensis gayi) on Oahu.

Location of Nests

One of the most interesting features of nesting is the nest location (tables 3 and 3a). Height (distance from nest to ground) ranges from 0.6 meters to over 30 meters (mean = 5.89 m). Distance to the base of the tree varies with the type of tree but distance from the nest to the tip of the branch averages 52.9 cm and is less variable. Nests are usually located in thick terminal clumps of vegetation, well protected from the rain and sun. The wind direction is related to the location of nests also. In trees exposed to the wind (not protected by buildings), nests were located in the windward side of the tree only 10 out of 77 times.

Specialization in placement of the nest is not uncommon for tropical birds. Ricklefs (1969) states: "In the tropics, numerous species construct domed or pensile nests, choose special localities, as over water, and have evolovednesting relationships with termites and wasps. Thus, nest construction and placement of some species is more specialized than in temperate regions. The same may be true of adult behavior." The White-eyes seem to fit this category.

A highly variable factor in nest location is the type of vegetation in which the birds build. I found nests located in 42 species of trees and shrubs on campus (see table 3). Individual pairs seem to show little preference for a particular tree type, and most pairs built consecutive nests in different types of trees. However, one pair built at least one nest in 1973 in exactly the same place as one of their 1972 nests. Furthermore, a pair in 1973 built two out of four nests on the same branches of two different trees, as a different pair had in 1972. This points to the specialization of nest sites, even within a wide variety of trees.

Table 3

Vegetation in which Nests were Constructed
1972-1973

Common Name	Scientific Name	Number of Nests
Haole Koa	Leucaena leucocephala	23
Banyan	Ficus retusa	22
Fiddlewood	Citharexylum spinosum	6
Monkeypod	Samanea saman	5
Hybiscus tree	Montezuma sp.	4
Opiuma	Pithecellobium dulce	4
Bamboo	Bambusa sp.	3
Flame tree	Brachychiton acerifolium	3
False Olive	Elaeodendron orientale	3
Mango	Mangifera indica	3
Mock Orange	Murraya exotica	3
Acacia	Acacia sp.	2
Ironwood	Casuarina equisetifolia	2
Green Ti	Cordyline terminalis	2
Silver Oak	Grevillea robusta	2
Queen Flower tree	Lagerstroemia speciosa	2
Panax	Nothopanax sp.	2
Avacado	Persea americana	2
Strawberry Guava	Psidium cattlelanum	2
Pink Tecoma	Tabebuia pentaphyla	2
Kukui	Aleurites moluccana	1
Octopus tree	Brassaia actinophylla	1
Yellow Shower	Cassia fistula	1
Pink Shower	Cassia javanica	1
Pink Shower	Cassia grandis	1

Table 3 (cont.)

Common Name	Scientific Name	Number of Nests
Coconut Palm	*Cocos nucifera*	1
--------	*Cordia* sp.	1
Cypress	*Cupressus semper virens*	1
Eucalyptus	*Eucalyptus* sp.	1
Banyan	*Ficus benghalensis*	1
Banyan	*Ficus religiosa*	1
Banyan	*Ficus umbellata*	1
Fern tree	*Filicium decipiens*	1
Hybiscus	*Hybiscus* sp.	1
Wood Rose	*Ipomoea tuberosa*	1
Litchi	*Litchi chinensis*	1
Paperbark	*Melaleuca leucadendron*	1
Guava	*Psidium guajava*	1
Kiawe	*Prosopis pallida*	1
Christmas Berry tree	*Schinus terebinthifolius*	1
African Tulip	*Spathodea campanulata*	1
Tecoma	*Tabebuia pallida*	1

Total number of nests	119
Total number of plant species	42

Table 3a

Location of Nests Within a Tree*

	Distance from Branch Tip to Edge of Nest (in cm)	Distance from Nest to Base of Tree (in meters)	Height of Nest from Ground (in meters)
Mean	52.9	2.11	5.89
Standard Deviation	26.0	62.37	3.68
Number	29	5	91

* No significant difference between 1972 and 1973 measurements (t-test).

Nest Construction

Nest construction of one nest located in a Fiddlewood tree (Citharexylum spinosum) is outlined below. It was the second nest of the 1973 season. The first brood had fledged 15 days before.

Day 2--A few bits of spider web were at the nest site when I found the nest. The birds visited the site three times from 0750 to 0910, and both came to the nest with the fledglings. The young were fed about three meters from the nest. Of the three trips, nesting material was brought only once.

Day 3--Much more material at the nest site. During a 30-minute observation period the nest was visited 12 times. The outline of the cup started.

Day 5--Nest still at the same stage as on day two. The fledglings were fed once in the tree next to the nest tree. Seven trips were made to the nest in 20 minutes, but only one with nesting material.

Day 9--Nest complete with the first egg. The fledglings nowhere around. Adults not making regular trips to the nest.

At some nests, the adults will carry nesting material well into the incubation period. The time to complete the nest is usually about seven to ten days, but at the beginning of the season I observed a banded pair carrying material 31 days before completing the nest. Furthermore, at the beginning of the season and late in the season, I have found nests partly constructed that were abandoned for no apparent reason (four in the end of 1972 season and two at the start of 1973 season). This phenomenon is possibly due to low reproductive "drive", and has been reported for other passerine species (Nickell, 1951).

An interesting behavior was observed at five different nests.

Birds would move their nest to a new site. In at least four cases this was after I had been to the nest, suggesting that I may have disturbed the birds. It occurred during the nest building period. In these cases, the birds removed the material, piece by piece, from the old nest and reassembled it at the new site. One pair moved their nest twice before laying eggs. This has been reported for other passerine species (Nickell, 1951). The second nests took no less time to construct, and I could find no significant difference in the distance the second nest was located from the first nest in nests dismantled as described above, and when nests were completely abandoned during nest building (see table 4).

I made no attempt to analyze the different movements of the birds during nest building. Kunkel (1962) described the technique of *Z. palpebrosa* as typical of birds whose nests are suspended between twigs. They work from the inside of the nest, and while the cup is being formed they often sit inside the cup and push with their breast.

A first nest built by a 1972 juvenile was one of the most 'regular' nests found. The cup depth, diameter, bottom thickness, and rim thickness were almost exactly at the mean of the total population. This suggests that the birds need little practice to know which material to select, or else the mate of the 1972 juvenile (it was unbanded) was an experienced bird. I have found no evidence of juveniles building nests or helping with their parents' nests before maturity, but they would be able to watch.

Spacing of Nests

The distance between active White-eye nests averaged 188.16 meters (range of 15 meters to 854 meters). More regular in spacing was the distance between song positions. I have observed two nests as close as 15 meters, but the distance between the song positions was 40 meters. This averaged 91.9 meters (see table 5).

Interspecific spacing of White-eye nests and other species nests may be very small. I have observed active White-eye nests 8.1 meters from a Linnet (Carpodacus mexicanus frontalis) nest, 5.7 meters from an active Mynah (Acridotheres tristis) nest, 2.1 meters from an active American Cardinal (Cardinalis cardinalis) nest, and 1.8 meters from an active House Sparrow (Passer domesticus) nest.

Interspecific defense of the nest was not observed. In 1972, I observed the interuption of two White-eye nests by House Sparrows. The Sparrows began to build a nest in a Pink Tecoma (Tabebuia pentaphyla) tree where a White-eye nest with three young was located. The male House Sparrow pecked the young to death two days after being first observed in the tree. At a White-eye nest in a Monkeypod (Samanea saman) tree, a male Sparrow was observed pecking at the nest the day before it was abandoned. The nest was inaccessible so I don't know if it contained young or eggs. In both cases the White-eyes offered no resistence, and in the former case carried food to the nest for a full day after the young were dead.

~~Several interactions were~~ noted between White-eyes and Red-vented Bulbuls (Pycnonotus jocosus) during the course of this study. At an Autograph (Clusia rosea) tree where the Bulbuls were feeding, several White-eyes attempted to chase the birds away. This was observed on two different days, and in both cases the Bulbuls ignored the White-eyes and continued to feed. I observed a pair of Bulbuls successfully chase several White-eyes out of a Monkeypod tree where the Bulbuls were constructing a nest, but they also chased Mynahs and House Sparrows away.

Table 4

Distance Between Consecutive Nests of Individual Pairs *
(in meters)

	When First Nest is Torn Down; Distance to the Next Nest	When first Nest is Successful; Distance to Next Nest	When first Nest is Abandoned; Distance to the Next Nest
Mean	63.64	18.70	44.50
Standard Deviation	37.44	20.04	35.59
Number	5	8	3

* No significant difference between 1972 and 1973 measurements. See text for further discussion.

Table 5

Distance Between Active White-eye Nests and Active Song Posts *
(in meters)

	Distance Between Active White-eye Nests	Distance Between Active Song Posts
Mean	188.16	91.94
Standard Deviation	250.52	38.40
Number	15	126

* No significant difference between measurements of 1972 and 1973. See text for further discussion.

Description of Eggs

Eggs belonging to birds of the genus *Zosterops* are typically immaculate and vary from white to very pale blue (Van Tyne and Berger, 1971). In the literature there are reports of colors ranging from a pink-white to blue-green-white (Moreau, 1955; Skead and Ranger, 1967; Vincent, 1949). The color difference has been attributed to individual variation. However, I discovered that there is a color change with the age of the egg. When newly laid, the eggs are a transparent white, and at times look slightly pinkish. As incubation proceeds, the eggs become more opaque (probably due to the developing embryo), the color appears to become darker and seems bluish. If the nests were not checked several times during incubation, and several were found at different stages of incubation, it would appear that the color variation was great within the species.

In 1908, Ingram described the eggs of *Z. japonica* as being 0.65 x 0.5 inches (16.5 x 12.7 mm). This is well within the range of what I found for the species in Hawaii. The mean size of 35 eggs from 1972 and 1973 is 16.5 x 12.6 mm. There was no significant difference between the egg measurements of the two seasons (t-test; see table 6).

Clutch Size

The mean clutch size for the two seasons is 3.14 eggs. I found several nests with two eggs, and one nest of five eggs near Makapuu Point was found by W.Y. Brown in 1972. All other nests held three or four eggs. There was no significant difference between the two seasons (t-test).

Table 6

Egg Measurements *

	Width (in mm)	Length (in mm)	Weight (in grams)	Clutch Size
Mean	12.65	16.52	1.31	3.14
Standard Deviation	0.52	0.68	0.13	0.98
Number	35	35	20	25

* No significant differences in measurements of 1972 and 1973.

Laying, Pipping, and Hatching

In 1952, Skutch reported that the time of laying, for a particular locality and species of bird, is usually standard with little variation. The hatching time is somewhat more variable, but usually occurs more often in one quarter of a 24-hour day. This seems to be the case for White-eyes. Nine eggs in five nests were laid between sunset and the morning of the following day. For exact times see Table 7. At one nest the last egg of a three egg clutch was laid between 0633 and 0645. I have no evidence of any egg being laid later in the day, and in light of Skutch's paper, I feel laying time is early morning. It probably is not during the night, since the female does not sit on the nest at night until after the third egg (usually the last egg) is laid.

Hatching usually is either at night or early in the morning. I checked seven nests the evening before hatching and again the next morning, and determined the following. In four nests eggs were not hatched before 1800, 1700, 1800, and 1700, and not after 0715, 0635, 0900, and 0830 the next morning. Only one hatched during the day. It was part of a three egg clutch. Two hatched between 1700 and 0635, and the third between 0635 and 1900.

Signs of pipping may appear as long as 24 hours before hatching, as small cracks at the large end of the egg, near the long diameter of the air sac (see fig. 2). As a rule all eggs are pipped the evening before hatching.

Ageing of the Eggs

Several techniques have been developed for determining the age of eggs (i.e., measuring the weight loss during incubation, candling to determine embryo size; Westerskov, 1950). However, the eggs of

White-eyes are so small, that with the scales I was using, I could not determine weight loss accurately enough to age them. Candling would probably be useful, as the shells are transparent enough to see through with little light. The easiest method I discovered was measuring the size of the air cell at the large end of the egg.

Westerskov (1950) discussed the use of this technique in pheasant eggs. During incubation, the evaporation of water from the egg and the shrinkage and solidification of the egg contents into a chick cause a gradual growth of the air cell. In the White-eye egg this cell is easily visible through the shell of the egg, and the diameter is easily measured. The age can be determined to within two or three days, and the relative age of the eggs within a clutch is easily found. The oldest egg (laid first) has the largest circle, and the last has the smallest. In five nests, I found only one egg to be an exception. The circle was not round, and it was difficult to determine what size the diameter was. The circle size increases in eggs that do not hatch also. I have diagrammed the air cell diameter on different days of incubation in Figure 7.

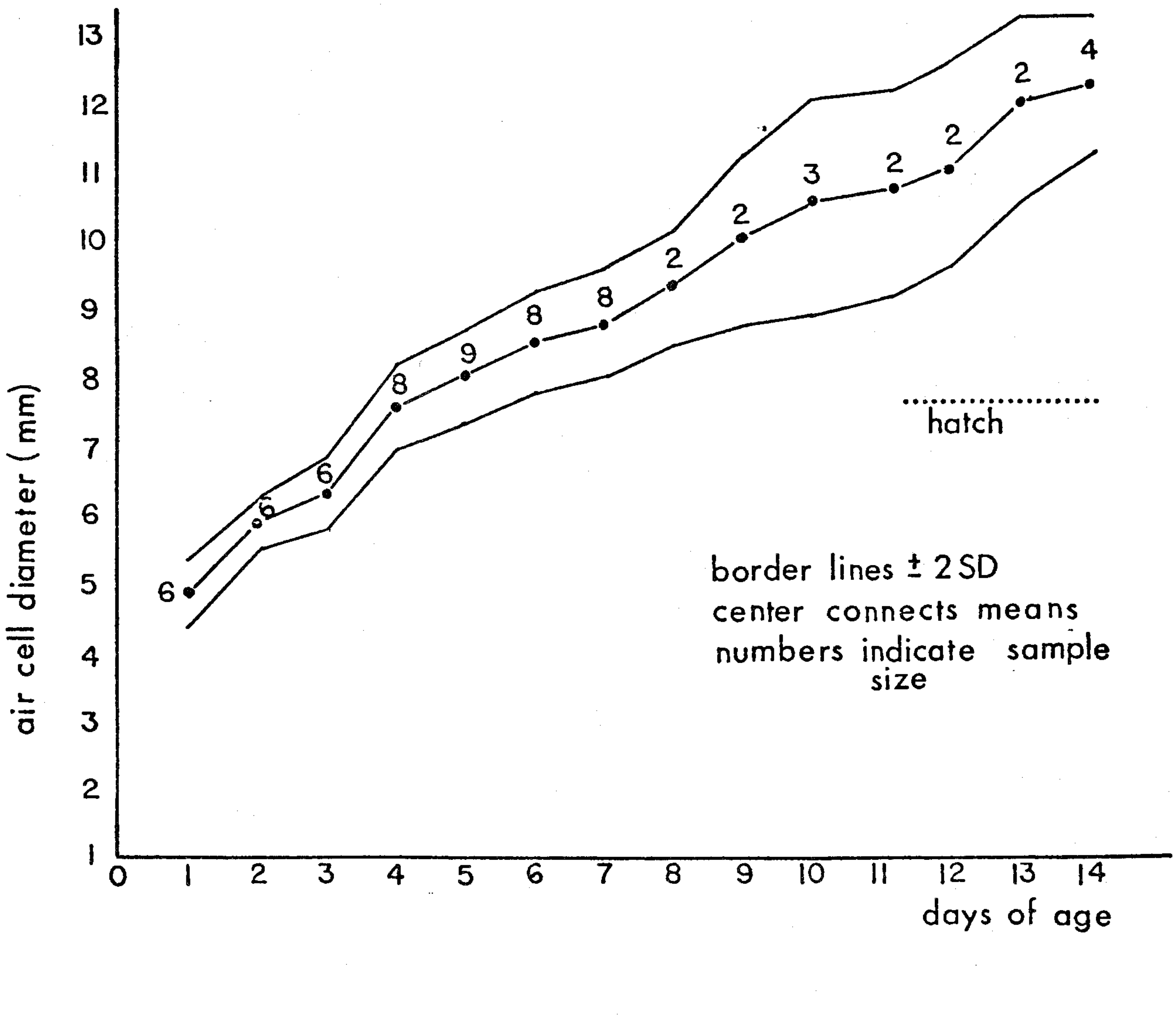


Figure 7. Air Cell Diameter in Relation to Age of Eggs.

Incubation Period

Incubation period is defined as the time which, with regular incubation of a newly laid egg, elapses until the young has left the egg. A practical definition is the time from the laying of the last egg to the hatching of the last egg when all the eggs hatch (Nice, 1953)

This subject has been the subject of much discussion in the literature concerning *Zosterops*. In 1953, Nice wrote, "*Zosterops*, the White-eye or Silver-eye, has attained world-wide fame for the shortest period of any bird--9 to 10 days. This rumor started in a careless observation in New Zealand in the 1880's. In eleven or more nests that have been carefully watched from 1870 to 1943 the incubation period lasted 11 to 12 days."

In this study I measured the incubation period at four nests, in which all the eggs hatched. The results are presented in Table 7. Assuming hatching occurs in the morning, the incubation period is 11 days in all four cases. However, if hatching occurs at night, it could be as short as 10 days and 10 hours. I feel that hatching probably occurs in the morning.

Nestling Period

"A young bird is a *nestling* from the time it hatches until it leaves the nest" (Berger, 1961). In the literature *Zosterops* is said to have a nestling period varying from 9 to 13 days (Davidson, 1952; Gilliard, 1967; Wilkinson, 1931). I found it to be between 9 and 10 days at six nests that were not disturbed from day eight to fledging. If the nest is disturbed (i.e., by daily weighing of the young), the chicks may leave a day early.

Table 7

Incubation and Nestling Periods

Nest Number & Year	Laying of Eggs	Begin Incubation (morning)	Hatching of Chicks	Fledging from Nest	Incubation Period	Nestling Period
31-1972	May3,0900* May4,1700* May5,1100*	May 5	None at May15,1800; All by May16,0715*	May 26, 1435	10 days, 17 hours, ± 6 hours	10 days, 13 hours, ± 6 hours
24-1972	Apr. 26 Apr. 27	Apr. 27	All by May 8,1730*	----	11½ days, maximum	----
35-1972	---- ---- ----	----	All by May 12	May 21, 1100	----	9 days, 2 hours, ± 4 hours
10-1972	---- ---- ---- ----	----	Two by Mar21,1630; one by Mar. 22,1100; one no hatch.	Mar.31, 1430	----	9 days, 13 hours, ± 10 hours
60-1972	---- ---- ---- ----	----	All by June12, 1214*	June 22, 1007*	----	9 days, 12 hours, ± 10 hours
14-1973	Two by Apr7,1230; One on Apr8,0900*	Apr.8	None at Apr18,1800; All by Apr19,0900*	----	10 days, 18 hours, ± 8 hours	----
9-1973	Two by Mar17,1100; One Mar18, between 0633 & 0645	Mar18, 0645	Two by Mar29,0635; One by Mar29,1900	Apr. 7, 1200*	11 days, 6 hours, ± 6 hours	9 days, ± 7 hours
12-1973	Two by Mar. 31, Two by Apr. 10	----	None at Apr12,1700; 3 by Apr.13, 0830; one no hatch	Apr. 22, 1000	----	9 days, 9 hours, ± 8 hours

* this time represents the first or last time a nest was checked on a particular day, therefore it is a minimum or maximum time.

Nest Attentiveness

Nest attentiveness is defined as the actual time spent at the nest by either or both members of a pair and the periodicity of such time (Baldwin and Kendeigh, 1927). In the White-eye both sexes are reported to incubate and feed the young (Van Tyne and Berger, 1971), and I could find no difference in the behavior of male and female at the nest. There is no ceremony at the nest when the birds relieve each other.

I determined constancy on the basis of the formula given by Skutch (1962) where $T = \frac{100\ S}{S + R}$; and T = percent constancy, S = total time in sessions at the nest, and R = total time in recesses from the nest. I modified the equation slightly by taking the total time the bird was at or away from the nest during an observation period, rather than only using complete recess and session time. Furthermore, I determined percent attentiveness for each nest observed, and averaged these percentages to determine the mean constancy for any one day of incubation and nestling period. In this way no one nest contributed more than another, even though it may have been observed for a longer period of time. It is this final mean that is plotted in Figure 8.

Start of incubation is noted by an increase of nest attendance (from 40% to near 100%) and then there is a slight drop on the second and third day. Skutch (1962) states that in passerines constancy is often less at the beginning of incubation, especially in the tropics, and gives the example of a Bushtit with 43.5% constancy on the fourth day of incubation. This might explain the drop in nest attendance on the second and third day, but the number of nests observed is small, so caution must be used in interpretation.

The overall attendance remains high during incubation, even with the above mentioned drop on the second and third day. It is above 70% for all days, and above 80% for all but the second and third day. Constancy decreases from the day of hatching until it reaches 0% on the ninth day. Incubation at night continues until the eighth night.

Related to the nest attendance is the length of sitting bouts (fig. 9). In determining the mean lengths on various days, again I allowed no one nest observation to contribute more than another to the final mean. During the incubation period the bouts ranged from 9.5 to 40 minutes.

Skutch (1962) reports several factors that may affect the length of a sitting period: activities of the mate nearby; type of food a species eats; weather. I have observed sitting White-eyes leave the nest to join their mates, feed and/or preen. The White-eyes eat a variety of fruit and insects, but I have observed no courtship feeding (reported for Z. palpebrosa; Kunkel, 1962). Food may help determine the length of sitting bouts for the species. Also length of the attentive periods decreases during the nestling period. This is undoubtedly related to the increased rate of feeding. As more trips are required to bring food as the chicks grow, the sitting bouts must decrease in length.

Adverse weather and rain increase the constancy of incubation. I observed this phenomenon at one nest, in early 1973. There was very bad weather throughout the incubation and nestling period. I did not find the nest until the fifth day of incubation, but constancy for the following days was: Day 5, 90%; Day 6, 100%; Day 7, 100%; Day 8, 100%; Day 9, 100%; Day 10, 97%; Day 11, 100%. These figures all represent at least one hour observation with the exception of day 9. On day 9 I observed the nest for only 40 minutes. During the nestling period the attendence remained much higher than normal. On day 7 the constancy was 100% (43 minutes of observation) and on day 8 it was 97% (46 minutes observation). On day 9, when I have never observed brooding at any other nest, the percent constancy was 94% (30 minutes observation). Because of the high rate of attendence, the rate of feeding was far below normal, and the chick lost weight on the third day and never reached "normal" (—2 standard deviations below the mean). Brooding continued to day 13 when the parents abandoned the nest. The chick died in the nest on day 14.

The nest was in a very exposed place, and the wind very strong. It rained every day, for at least a portion of the day. There were originally two eggs, and two hatched, but one chick was gone from the nest on the second day of the nestling period. There were several nests of different pairs that built in less exposed places during this session of bad weather that were completely successful.

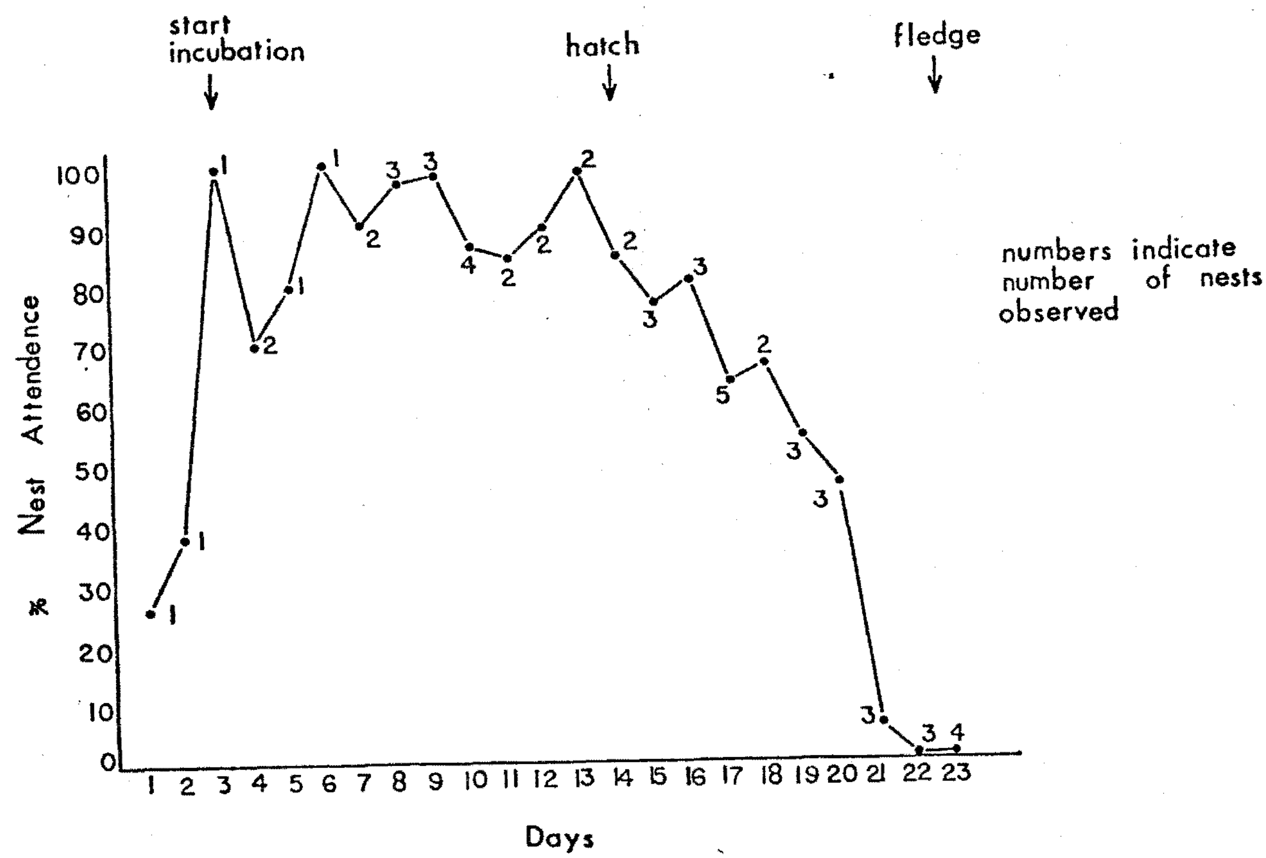


Figure 8. Percent of Time the Nest is Attended.

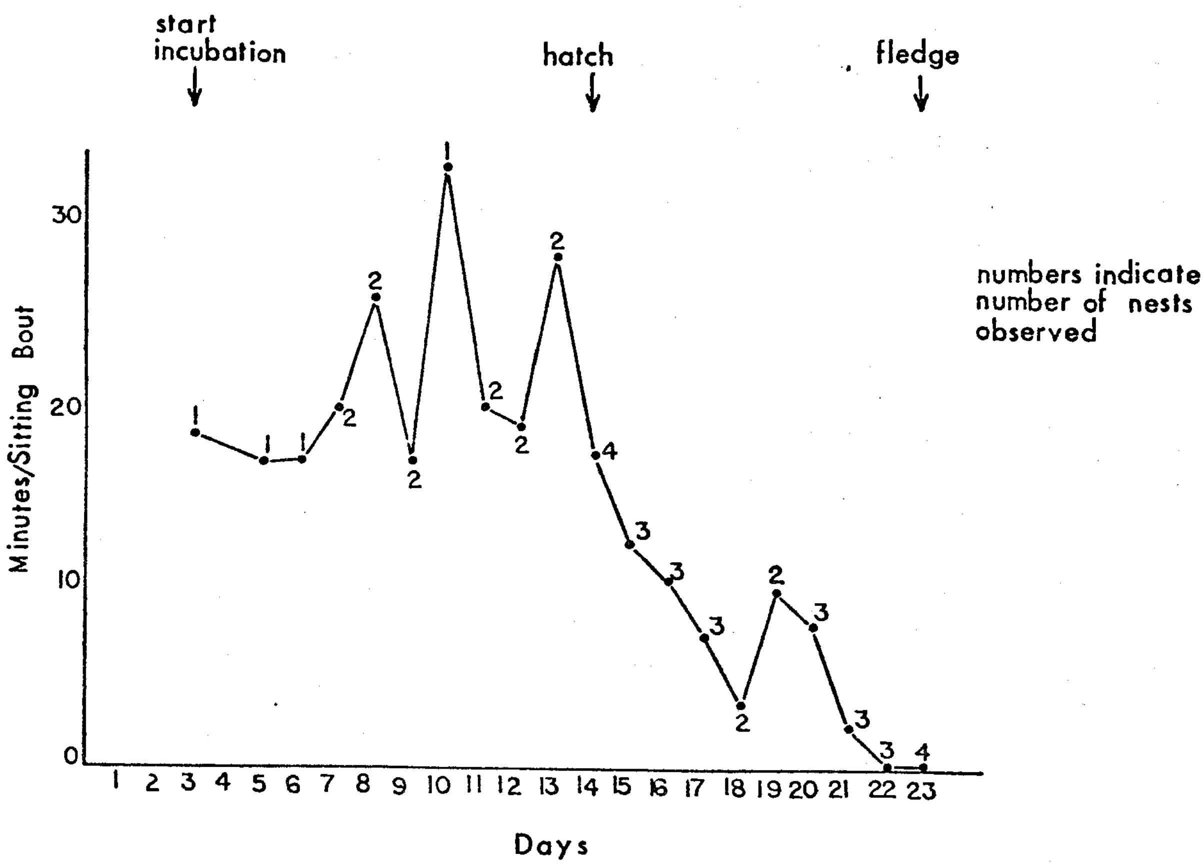


Figure 9. Length of Sitting Bouts in Relation to Nesting Cycle.

Feeding of Nestlings

Both parents carry food to the young. The young gape when the parents alight or land on the nest rim, apparently in response to the mechanical movement of the nest, as they will gape readily if the nest is tapped gently. The parents then place the food deep in the throat of the nestlings, and the young swallow. In the latter part of the nestling period the young become vocal as the parents approach the nest. At fledging they begin to wing quiver while begging. I observed feeding in detail at 10 - 15 nests, and measured feeding rates at three nests.

Nestling food was not analyzed in detail; however, at one nest I was able to observe from a close distance and identify some of the food given to the young: Day 1, two inch worms (Lepidoptera), two flying insects; Day 2, a grasshopper; Day 6, two figs from a Banyan (Ficus sp.) tree, a Mock Orange (Murraya exotica) fruit, fruit from an Octopus (Brassaia actinophylla) tree. These data suggest that there are more insects fed early in the nesting cycle, but there is not enough evidence to make a strong statement. Davidson (1952) found a similiar situation in that insects and green catepillars formed most of the diet of White-eyes until the day before fledging when rasberries were fed.

The feeding rate increases from approximately one or two feedings per hour on the first and second day after hatching to as many as 14 feedings per hour two days after fledging. Data for three nests are plotted in Figure 10, and the regression line (slope =0.177).

The progressive increase in feeding rate is understandable in that when the chicks are newly hatched, the "chief need is not food but warmth" (Van Tyne and Berger, 1971). Food becomes more important as the birds mature. Furthermore, Ricklefs (1968) points out that the food processing organs may not be as efficient in a newly hatched bird as later.

Figure 10 shows the feedings/ hour/young, but the rate at which food is brought to the nest by the adults varies with the number of young in the nest, to a certain extent. This phenomenon has been shown to be true for other species of passerines (Skutch, 1949). At one nest, two young were lost (probably eaten by a lizard; see page 67) and the parents were left feeding only one chick instead of three. The rate at which the adults brought food decreased from what is normal at a nest with three young, on the second day after loosing the young. However, on the first day that the young were lost, the parents brought food four times in one hour and the chick accepted it only three times. For the entire sitting bout, the adult held the food in its bill, and flew with it at the end of the bout. On the third day, food was refused twice in a half hour period by the chick and again the parent held it in the bill. This was not observed on any consequent days, and the rate of carrying food was equal to what the chick accepted.

Eddinger (1967,1970) described White-eyes as feeding helpers (any bird which assists in the feeding of another individual other than its mate or offspring; Skutch, 1961). He reported immature and adult birds feeding other nestlings (White-eyes, Linnets, and House Sparrows) in his aviary. I found that in 1972 the birds in my aviary readily fed several fledglings introduced to the cage, but in 1973 the same birds ignored a White-eye fledgling introduced to the cage. Several years ago I had a fledgling in a cage in my apartment, and about seven or eight wild birds carried food to the window, but would not enter the house to feed the chick. In 1973, H. Eddie Smith (personal communication) told me of a White-eye feeding a linnet nestling at a linnet nest at Diamond Head. I have not observed White-eyes feeding young other than their own in the wild. I feel this is not a common behavior in the wild, occuring infrequently or in unnatural conditions such as an aviary.

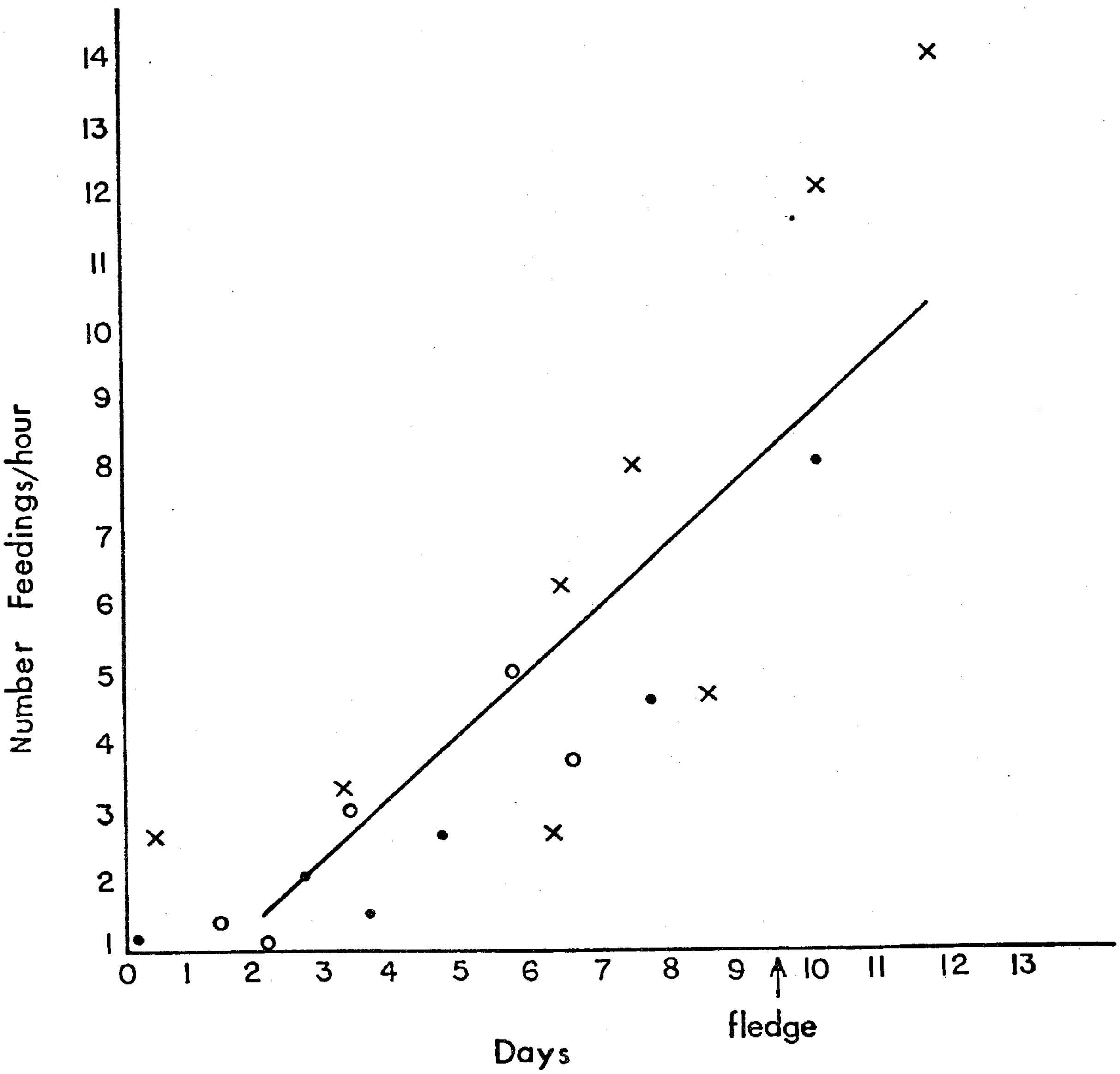


Figure 10. Feeding Rate of Young in Relation to Age of Young. Three different nests were observed (represented by different symbols on graph), and each symbol represents at least one hour observation. The regression line is plotted with a slope of 0.177.

Development and Growth

The White-eye is altricial, hatching naked (except for two small tufts of down over the eyes) and helpless. Chicks open their eyes on the fifth day after hatching, and make vocalizations. They exhibit a fear response (crouching in the nest) and begin to preen on the eighth day, and will leave the nest if disturbed on the ninth day. The earliest I have observed birds peck at food on their own and bill wipe is four days after fledging (based on observations of four hand raised birds). I also observed the first successful head scratch on the seventh day after fledging, the first chittering on the eighth day, and the first water bath on the 12th day after fledging.

During the nestling period there is a gradual change in the relative abount of time spent in various activities. Based on observations of one nest and one hand raised bird I compiled the data shown in Figure 11. On the first day the birds do little except raise their heads and gape. On day six, even though the eyes are open, 94% of the time is spent sleeping. By day 10 a variety of other activities are common. They sit and look out of the nest, preen themselves, and begin to move about, but 46% of total time is still spent sleeping.

Feather tracts can be seen deep in the skin by the second day after hatching, and most are open by the tenth day. Not all the tracts appear at the same time, and generally speaking, those that appear first are the first to unsheath. The head is the last part of the body to become feathered, and it is not uncommon for the chicks to fledge with the head partially bald and/or still in pin feathers. This has been noted as common among other species of Zosterops by Moreau (1957).

The general daily development is outlined below. This is based on observations of six chicks at two nests.

Day 1--Chicks naked except for two tufts of gray natal down above the eyes; eyes closed.

Day 2--Feather tracts are visible deep in the skin; spinal, femoral, ventral, humeral, and wing feathers easily seen but the tract above oil gland much deeper; head completely naked except for down.

Day 3--All tracts visible, and the primaries, secondaries, and ventral tracts just beginning to push out of the skin.

Day 4--The first row of wing coverts (upper) out of the skin, and head tracts visible deep under the skin.

Day 5--Primaries are about 6-8 mm in length; eyes barely open.

Day 6--Femoral tract beginning to open; all ventral tracts opening.

Day 7--Head feathers and scattered feathers on the outer part of the leg are still under the skin; neck, auricular, tail feathers, anal circlet, submalar tracts still pins; spinal, humeral, primaries, secondaries beginning to open.

Day 8--Feathers on back open enough to give an overall green color to the chicks; fear response in some young; begging vocalizations common.

Day 9--Head tracts still not open, but all other tracts open; will leave the nest when disturbed.

Day 10--Head tract beginning to open; fledge; location call note.

Day 23--Eye-ring complete.

Day 30--Independent and indistinguishable from the adults.

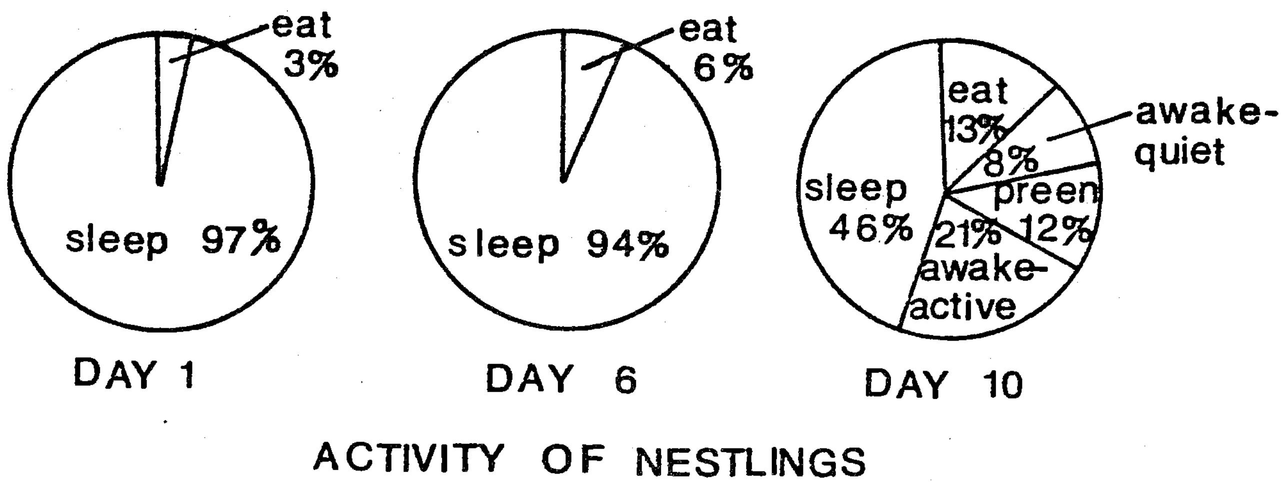


Figure 11. Each diagram represents one hour observation of one chick or one nest. Day 1 and 6 were observed at the nest, day 10 in the laboratory.

To measure the growth of chicks, daily weights were taken at several nests. About one gram per day is gained to the seventh day, and from day seven to ten (fledging) one more gram, giving 8.28 (average) grams total weight. The pattern is typical for a small altricial bird (Ricklefs, 1968). In Figure 12 I have graphed the growth curve.

Rapid growth rates and short nestling periods are not uncommon in small passerine birds. Lack (1968) suggests that growth rates are "ecological adaptations for breeding" and since growth requires energy, the rate of growth depends on how many young can be fed by the parents. As mentioned earlier, feeding rate of White-eyes increases to a very high point (about 10 feedings/hour at fledging). However, the weight gain at this point is leveled off. Whether or not there is a direct relationship between the number of young that can be fed and the growth rate in White-eyes, I can not say from my data. Ricklefs (1973) feels that energy requirements of the young are not balanced against brood size, based on a review of many bird species; rather growth rate is related to the precocity of development (those that develop late have rapid growth). White-eyes develope late (i.e., can't fly when leave the nest) and have rapid growth rates. There appears to be a slight decrease in weight at fledging. This is common in many passerine birds due to a loss of water (Ricklefs, 1968). However, this decrease is not significant in White-eyes (one-sided t-test).

The nestling period is about ten days (see page 46), and during that time the chick doubles its weight three times. At fledging the young are not able to fly well, but within three or four days after leaving the nest, are able to fly for short distances. At one nest I measured the distance a chick was able to fly on several successive days. On the day of fledging the chick fluttered from the nest to the ground, covering a distance of two meters. Two days later it flew seven meters and did not loose altitude (the wings were within the range of adult size). However, at another nest one young flew over 15 meters and gained a height of about four meters on the day of fledging, so there is some individual variation, but the ability to fly this well at fledging is very unusual.

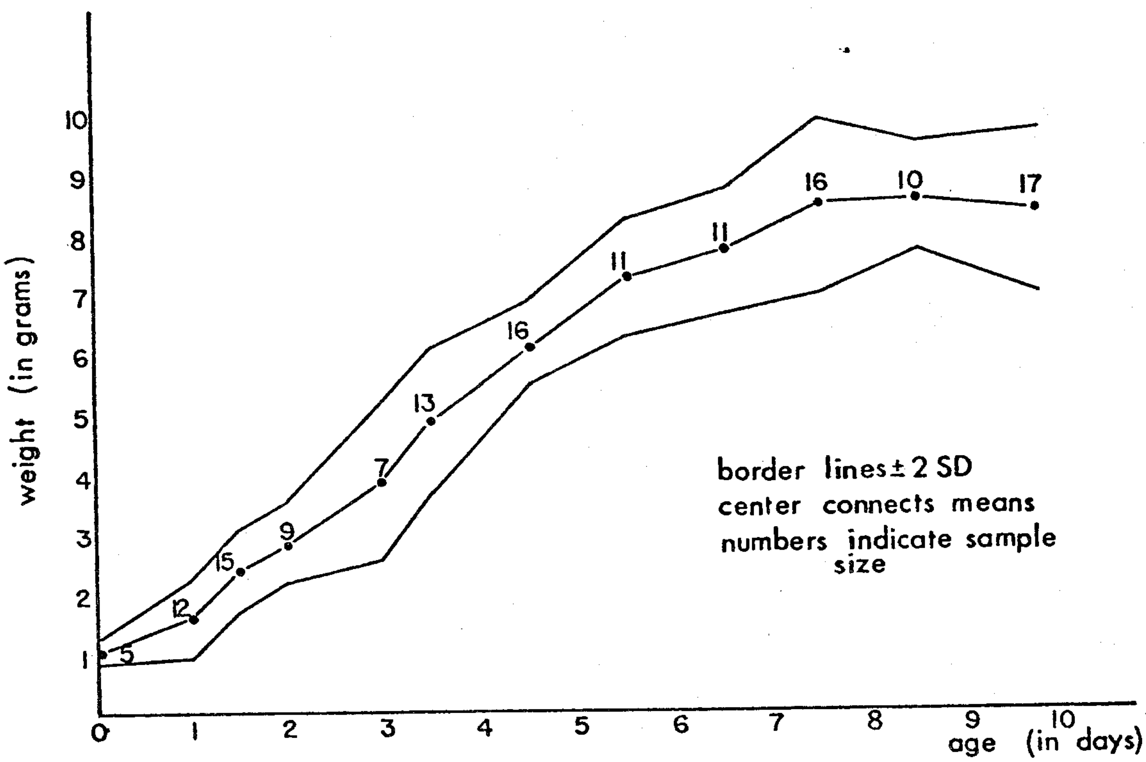


Figure 12. Growth-weight Curve in Relation to Age of Chicks. The data are from 1972 and 1973. There was no significant difference in data from the two seasons.

Nest Sanitation

Nest sanitation is complete. Generally speaking, for the first few days after hatching the fecal sacs(well formed, enclosed in a gelatinous membrane for entire nestling period) are eaten, and toward the end of the nestling period they are carried away by the parents. I have observed a fecal sac carried as early as the third day after hatching, and eaten as late as the ninth day after hatching. At one nest a chick defecated over the side of the nest without the parent retrieving the fecal sac on the day of fledging. By carrying the fecal sacs or eating them, there is no accumulation on the ground to reveal the presence of a nest.

Egg shells are probably carried away after hatching, but I have not observed this.I have found shell about ten feet from a nest on the morning of hatching when there was no wind. Foreign material in the nest is removed by the parents. Unhatched eggs remain in the nest, unless they are broken. For example, in the case of one four egg clutch, in which an unhatched egg was broken, the broken egg disappeared on the second day after the hatching of the other three.

Fledgling Period

The feldgling period is defined as that time from the leaving of the nest to complete independence of the young (Berger, 1961). In five cases, this period was between 15 and 23 days. It was exactly 20 days for one brood and between 19 and 21 days for another. On one occassion I observed the parents chase the young from their territory, and new nest, on the 26th day after fledging. Adults begin nest construction about one week before the young of the previous brood are independent. These findings are similiar to those reported in the literature for the genus Zosterops.

I observed actual fledging at only one nest. The young stretched and looked out of the nest, periodically during the morning, sleeping between active periods. At 1430 one of them was about seven centimeters from the nest, on the branch supporting the nest. The two birds in the nest hopped on the nest rim. When the adults approached with food, all three young begged and hopped up the branch toward the parents. They did not return to the nest.

At fledging, the parents become more vocal. For the first couple of days chittering is very common, and singing increases (see fig. 4). The young can not yet fly, and thus are rather vulnerable. If they flutter to the ground, both parents swoop and reach the ground with the chick. However, the adults fly past the young and invariably an observer watches the adults fly up from the ground, loosing track of the chick. This diversionary tactic is so predictable I often used it to catch the adults at the nest. I dropped the young in front of the net, causing the adults to swoop down and past the young bird, into the mist net.

Another diversionary tactic that I observed at one nest concerned a large dog that was in the area at the time of fledging of the young. Both adult birds flew about one meter above the ground and just ahead of the dog, and led it away from the young. After about 100 meters, the parents flew high in the air and returned to their young. Along these same lines is behavior which served to distract me when I observed a nest from too close a distance. One bird flies directly toward me or low to the ground conspicously, while the other slips to the nest. I have seldom seen the bird going to the nest, even though I am aware of what is happening. It always takes me by suprise.

After fledging, the young remain in the nest area. They cannot fly but hop and cling to branches. One newly fledged chick was placed on the floor of my aviary twice, and both times immediately hopped to the nearest branch and then hopped up the foliage until reaching the highest point in the cage. At one nest I found the young (two chicks) about ten meters from the nest on the day after fledging, and 15 meters from the nest three days after fledging. It is about one week before the chicks can fly and move well enough to follow the parents. They then move throughout the territory and general area as a family group, sometimes joining other family groups to form small flocks of six or seven birds. The parents feed the young until they become independent. This pattern has been true of every nest I have observed.

When the young become independent, they may remain together for at least a short period. I have few observations of juveniles once they leave their parents, but two chicks were found roosting together two days after becoming independent, near the nest tree (10 meters). Another juvenile was seen in a feeding flock of about 25 birds, 72 days after fledging (50 days after becoming independent) about one-half mile from where it had fledged. Two 1972 juveniles were found breeding in 1973, both within one-quarter mile from where they fledged.

Breeding Success

Adult mortality on campus may be fairly low. Of 28 birds banded on campus, that had a territory on campus, 18 (67%) were known to be alive at least four months later. No 'search' was made for these birds so the percentage may be higher than indicated. Sightings of juveniles were fewer. Of 23 fledglings banded at the nest in 1972, only two were found breeding in 1973. Whether this indicates that they move out of the area or die, I don't know.

I determined nesting success on the basis of percentage of eggs and young in individual nests, rather than total eggs or young. The percentages of success for each nest were then averaged to determine the overall success of the population. By doing this, large clutches do not contribute more to the success or failure figures than do small clutches. I found no difference in success related to clutch size, so I feel that this is important.

Of the eggs that were laid, 83.5% hatched over two seasons (based on 18 nests, 56 eggs for 1972 and 17 eggs, 6 nests for 1973). Eighty-two percent of the chicks that hatched, fledged (48 young, 19 nests in 1972; 16 young, 7 nests in 1973), and 58.6% of eggs laid, fledged (21 nests, 59 eggs in 1972; 14 nests, 33 eggs in 1973). There were no significant differences in the two seasons (t-test).

Nice (1957) found that open nesting, altricial birds in the North Temperate Zone average 49% success. Furthermore, Ricklefs (1969) states that "In general, birds of humid tropical regions are less successful breeders than temperate species." This means that the nesting success of the White-eye (58.6%) is very high. Each pair (potential average of three broods) would contribute 5.52 young to the population in a season.

Of the factors affecting the nesting mortality, weather was the most important. Six out of 33 nests failed due to the wind or storms. Poor nest construction and interference by animals other than man each contributed to the lowered success of three nests. In five nests, an egg or chick disappeared during the cycle, and I don't have data on the cause. Fifteen of the 33 nests were 100% successful.

Predation was observed in only one instance. H. Eddie Smith told me of a newly fledged White-eye that was resting in Haole Koa, about two feet from the ground. An albino mongoose was seen running from the stand of vegetation with the chick. The parents chittered, but to no avail.

I suspect predation in one case. At one nest two chicks disappeared from the nest on the same day I observed a large lizard (Anolis) within about one meter of the nest and on the same branch. I had been observing the nest daily, and had not seen the lizard present before or after the disappearnace of the young. I think they were probably eaten by the reptile. The young weighed only three grams, well within the size that the lizard could have easily eaten. Kikkawa (1962) reports that domestic cats are major predators on White-eyes in New Zealand urban areas. Penniket(1956) describes the predation on White-eyes by a White Heron.

Predation is probably one of the most important factors in the nesting mortality of most species (Ricklefs, 1969). While it was not observed often, there are indications that White-eyes have evolved behavorial measures to combat predation. The existence of diversonary displays, the selective nest-site, the moving of nests if they are disturbed early in the cycle, increase of singing (to make adults obvious) and increased chittering at fledging of the young, all point to the importance of predation. Whether or not the pressure is present in Hawaii, is difficult to say. There are rats that live in many trees that could serve as predators, along with the mongoose, other birds, cats, and etc. The fact that I did not observe predation often does not eliminate it as a potential factor of importance, because predation is typically seen seldom in the field.

Few parasites were found and little evidence of disease, but a thorough search was not conducted. In one juvenile bird found dead in June of 1972, there was a moderate infection of nematodes in the gut. In one chick, newly fledged, I discovered a heavy infection of coccidia. The bird was very weak and probably would have died had I not found it. (I took it to the laboratory, treated it, force fed it for two days, and it survived.)

Nest parasites were more numerous, but probably did not contribute significantly to the nesting loss. I found no evidence of chicks overly parasitized by nest fauna.

There were several other instances of White-eye mortality. In two nests the young became tangled in the fine nest lining and were unable to leave the nest at fledging. They were found dangling from the nest, and in both cases they died. At one nest, a young bird fluttered to the ground on the day of fledging, landed head-over-heels, and died. It probably injured itself when landing.

Abandonment of young occurred in two cases. The first is discussed on pages 49-50 in reference to affects of weather on nesting behavior. The other occurred outside my study area, in Waikiki. One chick hatched at least a full day after its three siblings, and was not able to compete for food. It did not fledge with the other three, and the parents stopped carrying food to the nest. It lost weight on several days, and was far below normal throughout the nestling period.

House Sparrows interupted two nests (see page 38). At one nest, the eggs were stolen by a student on campus, and I broke several eggs during the study. However, those nests,where I affected the success of the nest, were not used in determining mortality or success.

Table 8

Factors Contributing to the Failure of Nests
1972-1973

Weather	6 nests
Unknown and Miscellaneous	5 nests
Poor Nest Construction	3 nests
Interference by Animals other than Man	3 nests
Man (excluding me)	1 nest
* * *	
Successful Nests (100%)	15 nests
Total	33 nests

Table 9

Information on Banded Birds and Their Returns*

	Total Banded	Adults Banded	Fledglings Banded	Number Molting	Minimum Number alive after 4 months	Number Returned Dead
--1972						
January	0	0	0	--	--	0
February	20	20	0	0	5	0
March	32	24	8	0	4	0
April	6	4	2	0	3	2
May	25	14	11	0	6	0
June	0	0	0	--	--	0
July	9	8	1	4	2	0
August	11	11	0	9	2	0
September	0	0	0	--	--	0
October	0	0	0	--	--	0
November	0	0	0	--	--	0
December	0	0	0	--	--	0
--1973						
January	0	0	0	--	--	0
February	0	0	0	--	--	0
March	1	1	0	0	--	0
April	7	0	7	0	--	1
May	7	6	1	0	--	0
June	0	0	0	--	--	0
July	0	0	0	--	--	0

Table 9 (cont.)

	Total Banded	Adults Banded	Fledglings Banded	Number Molting	Minimum Number alive after 4 months	Number Returned Dead
August	3	3	0	2	--	0
--Total	121	91	30	15	22	3

* A total of 121 birds were banded over the 20 month period, and 17 known pairs had territories on campus. Seventeen birds caught during July and August of 1972 at Diamond Head are included in the above information, and molting information was obtained from them.

Summary of Breeding Success

The overall reproductive success of a population or species depends on a combination of factors, positive and negative. The interaction of these factors vary from season to season, with time of season, and even from individual to individual. In this paper I have outlined many of these factors, ahd their possible effects on the Manoa campus population, as a representative of any lowland, residential population of White-eyes. Among those factors that could act in a negative manner upon breeding success are weather, predators, parasites, food availability, interactions with other spceies, and accidents. In response to such pressures there are a number of positive factors that operate to increase the breeding success. Some of these factors are present in other passerine birds, but I feel that it is the combination of all of them that contributes to the success of the White-eyes. Following is a brief summary.

1. The overall mortality of adults seems low, and mortality of eggs and young is low for a small passerine bird.

2. The start of the season may be somewhat adaptable in response to environmental factors.

3. Birds are sedentary, of definite advantage to an island population.

4. Territory size is related to vegetation, allowing an efficient use of the available area for breeding.

5. Vegetation in which birds will build nests includes a wide variety of species.

6. Nests are difficult to locate, and well camouflaged.

7. The location of the nest is determined in relation to environmental factors.

8, No experience is necessary for first year birds to construct successful nests.

9. Development and growth are rapid, allowing several broods per season.

10. Young attain sexual maturity within one year, allowing rapid reproduction.

11. Birds mate for more than one season, perhaps for life.

12. Attentiveness can be modified in relation to weather.

13. Feeding rate of nestlings is somewhat adaptable, and can be modified to individual situations.

14. Both parents attend the nest and feed the young.

15. Parents exhibit defensive behavior that has survival value for the young.

16. Nest sanitation is complete.

General Behavior of White-eyes

A variety of behavior patterns are commonly seen in White-eyes. While I have never observed dust bathing, water bathing is common and was observed over 20 times in the wild. A leaky air conditioner on a roof was a favorite bathing location for White-eyes, Mynahs, Cardinals, Linnets, House Sparrows. Leaky faucets and water fountains were utilized also. White-eyes rub against wet foliage after a rain. One bird bathing usually stimulates other birds to bathe. Water bathing occurs once or twice a day in the aviary.

One hand-raised White-eye first water bathed when 22 days old and became so wet it could not fly. It followed the other five birds to the water pan for two days prior to actually getting in the water.

Sun-bathing also occurs commonly in the aviary. The birds hang from a branch or the cage near a warm light, fluff their feathers, spread wings and tail, open mouth, and extend the neck. I have not observed this behavior in wild birds.

Head scratching is done over the wing. In juveniles, there may be some trouble balancing during the first attempts. In one hand-raised bird, the first successful over-the-wing head scratch occurred 17 days after hatching, and in one bird, the day before leaving the nest. I have never observed White-eyes scratch under the wing.

Wing fluttering is discussed as a component of aggression, but was also observed during courtship and between mated pairs on five seperate occassions. Perhaps if analyzed more completely (i.e., on film) distinct differences would be evident. Juveniles also wing flutter as they beg for food.

Pairs roost together at night except when one is on the nest, and I have never seen more than two birds roosting at any one place. I have observed roosting on four seperate occassions. In the aviary, the birds roost in groups of two or three, or singly.

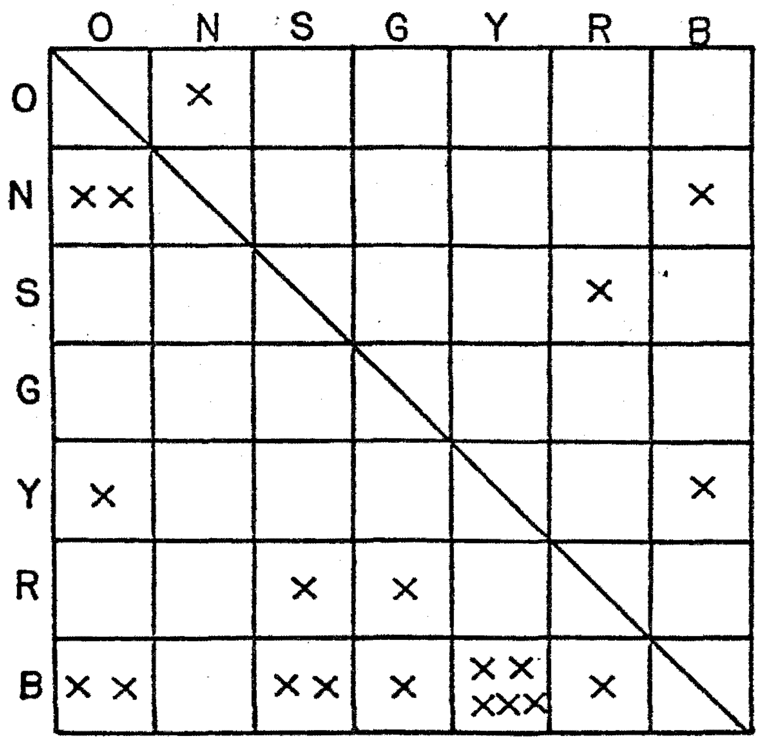
In terms of general behavior, it is noteworthy that White-eyes become tame very easily. Three wild birds that I captured all adapted very well to the aviary. Over the summer of 1972 I had occassion to keep 17 wild birds in a cage for about one month, and did not loose one bird. Furthermore, many of those birds have been recaptured since being released, indicating that they had no trouble readjusting to the wild. Young White-eyes are also easy to raise, providing they are fed often enough. I have not lost one (six have been hand-raised).

Flocking behavior is common in the winter season, and while resident birds usually remain near their home rnage or territory, I have seen large flocks of up to 100 birds. I don't know if large flocks are composed of mainly juveniles or adults. Some of the possible functions of this behavior is the easy location of feeding trees, and the observation for predators by many birds. Kikkawa (1962) found that in New Zealand residential areas, cats were the most important predators; and flocking behavior by the birds was effective in warning off attacks from cats. This flocking behavior could also be important in the dispersal of juveniles. Pair bond formation presumably occurs during the winter flocking.

Allopreening (= mutual preening) is very common in all species of White-eyes, and Kunkel found that in Z. palpebrosa and Z. virens it is dependent on dominance. He found an aggressive or dominant bird will only preen, and the other will only submit (Harrison, 1968). However, in Z. japonica allopreening is reciprocal, and extends over the whole body and tail. Furthermore, I could find no significant difference in the initiation of allopreening in relation to dominance except that, of the six birds in my aviary, the most subordinant engaged in allopreening more than any other individual (see fig. 13). This suggests that it is related to the hierarchy, but a more thorough analysis is needed. In some birds allopreening serves to decrease aggressive tendencies (Harrison, 1968; Sealander and LaRue, 1961). Possibly in my aviary, the most subordinant bird engages in allopreening more than the other birds to decrease aggression toward itself by the other birds.

Allopreening is very common in wild and aviary birds, and especially between mated pairs. Harrison (1968) suggests that it may be important in maintaining the pair bond. In White-eyes there is no sexual dimorphism, and few courtship displays other than allopreening. I feel that it is probably very important in the pair bond.

There is a very characteristic posture that the birds in the aviary assume when soliciting allopreening. The neck is stretched and all the feathers fluffed. Another bird will then fly to the solicitating bird and begin to preen. Quite often two or three birds will be autopreening next to each other and this will lead to allopreening.



ALLOPREENING

Figure 13. This diagram represents one hour observation of seven birds in an aviary. Each X stands for at least two bouts of allopreening, such that the bird in the left column initiated preening with the bird in the top row. The birds are arranged according to their position in the hierarchy (see fig. 14). "O", "S", and "G" are probably males, but this is not known for sure.

White-eyes as a group have very interesting aggressive behavior patterns that are easily observable in the aviary. This is one area that might warrant more research. There have been several behavorial studies on Z. lateralis (Kikkawa, 1961a 1961b, 1969) and on Z. palpebrosa (Kunkel, 1962) and I found the behavior of Z. japonica to be very similiar to that of the other species.

From aviary observations I was able to outline some of the features of aggressive behavior. The displays are composed of various components that are used in conjunction with each other to form a continuum, ranging from the most intense threatening to submissive behavior. Components probably correspond to modal action patterns (Barlow, 1968).

Components of threat behavior:

wing-fluttering--wings lowered and vibrated rapidly;

whine--nasal whining sound used in conjunction with displays;

chittering--scolding calls, used in conjunction with displays;

wing-flipping--wings raised and lowered rapidly in a flipping motion exposing the under-wing coverts which are lighter in color;

beak-clapping--bill is closed rapidly producing a snapping or clicking sound; probably a ritualized form of pecking;

open-mouth--mouth opened slightly and bill pointed towards opponent;

forward look--bird extends head and looks directly at opponent, probably emphasizing the white eye-ring; present in all threatening displays.

Components of submissive behavior:

fluffing--feathers of the body are raised; may include only a few feathers, such as only the crown of the head;

avoidence look--bird turns head away from opponent.

These components, in combinations and context in which they actually occur, are arranged from the most intense threatening behavior to the most submissive behavior in the following outline. These are based on aviary observations.

Display Components	Context
wing flutter wing flip whine beak clap open mouth forward look	Given in various combinations during actual attack and chasing.
wing flutter whine or chitter open mouth forward look	Preceeding or during chase. This series of components is probably comparable to the head-forward threat display common to most passerine birds (Andrew, 1961).
wing flutter beak clap open mouth forward look	Preceeding or during chase.
wing flip beak clap open mouth forward look	Displacing another bird at a feeding area, or preceeding chase.
wing flutter open mouth forward look	Displacing a bird at a feeding area, or preceeding chase.
wing flip forward look beak clap	Displacing another bird.
beak clap forward look	Displacing a bird or preventing one from landing too closely.
open mouth forward look	Preventing a bird from landing too closely.
fluffing open mouth forward look	Threatening of a dominant bird by a subordinant bird.
fluffing forward look	Submissive posture.
fluffing avoidence look	Submissive posture, and during allopreening.

Related to aggressive behavior is the existence of a hierarchy. Kikkawa (1961a) found evidence of a peck-right hierarchy in wintering flocks of Z.lateralis in New Zealand. I found a similiar hierarchy among seven White-eyes in an aviary. Furthermore, this hierarchy was stable over an entire year period. It was maintained by aggressive behavior as outlined above. See Figure 14 for a diagram of the hierarchy established among the seven birds in the aviary. The most submissive bird in the hierarchy was the oldest, and fed five of the others as fledglings.

A hierarchy in a winter folck could function to decrease the number of encounters between individuals, by the avoidence of dominant birds by subordinants. Also the feeding efficiency of all but the most subordinant might be increased through the existence of a hierarchy.

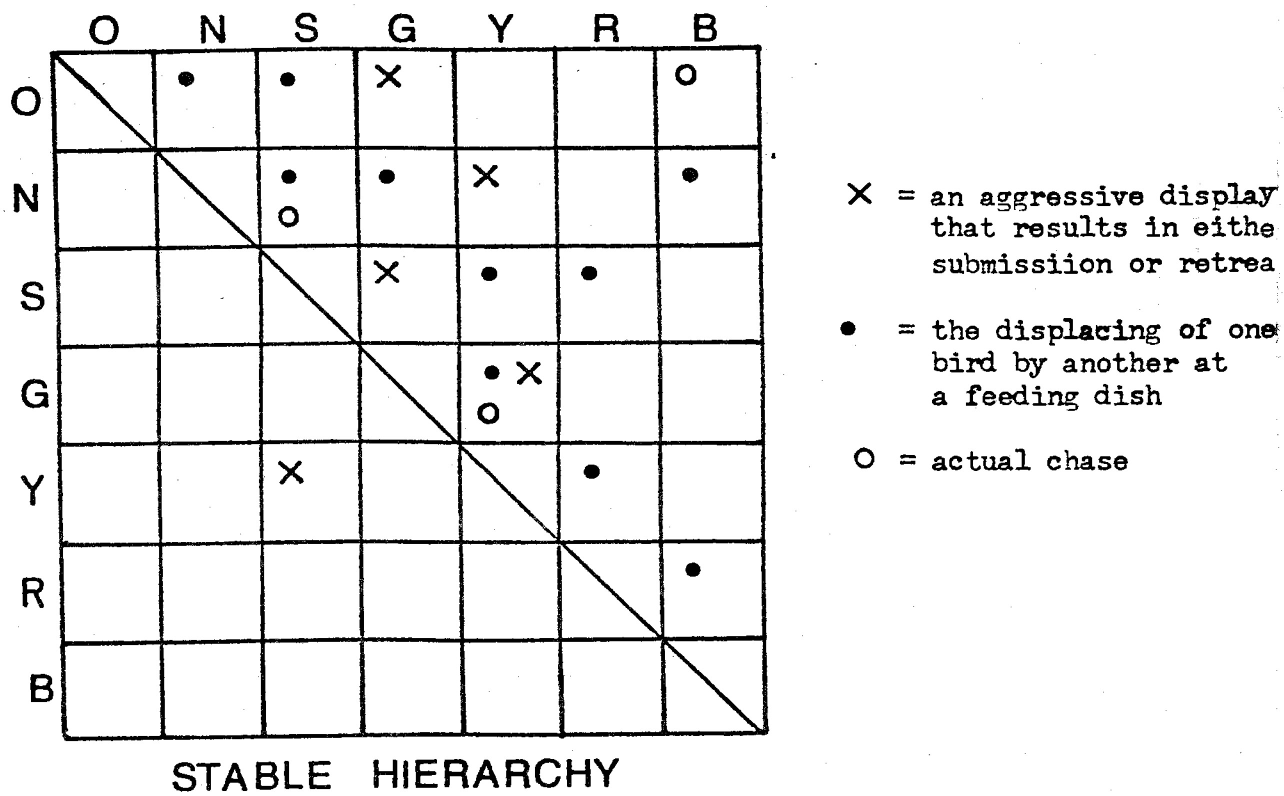


Figure 14. This diagram represents the hierarchy which developed in the aviary. It represents one hour observation, and each mark stands for at least two encounters. Each bird is represented by a letter. The birds in the left column interacted with the birds in the top row, such that the birds in the top row gave way to the birds in the left column. I am not sure of the sex, but "O", "S", "G", sang in the aviary and are probably males. However, the song differed from the normal territorial song of wild males. "Y" was the only bird to show aggression up the hierarchy. If this is a high ranking female, these results are similiar to those obtained by Kikkawa (1961a). "O" and "N" spent a lot of time allopreening, and I think they may have been a pair.

Adult Measurements

Measurements of adult birds are presented in Table 10, and include the mean and standard deviation for culmen length, tarsus length, eye-ring width, wing and tail length. Such measurements are used to sex some bird species, but I did not have enough positive information on which birds were male and female to even approach the problem. However, in the case of six pair, in which I was able to weigh both the male and female, the mean difference in weight from the heaviest to the lightest is only 0.51 grams (range from 0.0 to 1.1 grams). This is much less than the standard deviation of adult weight (1.55 gms), so it appears that there is probably no significant difference in male and female weight.

Marples (1945) found a seasonal change in weight in Zosterops lateralis, such that the birds weighed more during the coldest part of the year. Unfortunately, my data are incomplete during the coldest season here. I could find no significant difference in weights from 1972 and 1973 (t-test).

It has been suggested that the white eye-ring is used in aggressive displays (Kikkawa, 1961a), and this is in accord with my findings. Also the white under the wing is probably used in displays such as wing flipping. The green color of the birds seems to be adaptive, in that the birds are arboreal. All one has to do is try to search for the small green birds in a large green tree to appreciate how they are able to disappear in the foliage.

Table 10

Adult Measurements*

	Weight (in gms)	Tarsus Length (in mm)	Culmen Length (in mm)	Eye-ring Width (in mm)	Wing Length (in mm)	Tail Length (in mm)
Mean	11.25	20.40	10.72	1.42	59.40	41.00
Standard Deviation	1.55	1.55	0.82	0.12	1.6	2.0
Number	32	2	5	4	5	3

* No significant difference in measurements from 1972 and 1973. These measurements are from wild-caught bird.

Diet

Members of the Zosteropidae have omnivorous feeding habits, eating many varieties of fruit, nectar, and insects. In Australia, White-eyes are considered destructive among the fruit growers for the damage sustained to crops, and are known by the common name of blightbird (Wilkinson, 1931). However, many feel the fruit eaten by the birds is small compared to the destructive insects devoured by the birds (i.e., aphids and scale insects; Chisholm, 1908).

In Hawaii I have made many field notes concerning the food that White-eyes eat. Table 11 gives a list of the fruit and nectar that I have observed eaten in the field. I have included only that fruit or nectar which I have actually seen the birds swallow. In the case of nectar, it was difficult in most cases, to determine if the birds were eating insects at the flowers or drinking the nectar, therefore, many plants visited regularly are not included. When drinking the nectar of flowers the birds commonly split the base of the corolla with their bills, to reach the nectar. The tongue does not form a tube, but is quadrified and fimbriated both at sides and tip (Moreau, Perrins, and Hughes, 1970).

White-eyes also feed commonly on flying insects (i.e., termites) and spend much time foraging in the vegetation. Inch worms, army worms, and adult moths are common food items. The gut content of one juvenile bird found dead on the campus at 0830 on June 9, 1972 included one insect from the order Neuroptera (Chrysops sp.), and one unidentifiable insect, and unidentified plant material.

As to the destructive ability of White-eyes concerning fruit crops, I imagine it could be great. I have seen tangerines still on the tree that had no fruit left, consisting of only the tough skin.

However, Cardinals, Linnets, and Mynahs were in the tree also, feeding on the fruit. White-eyes eat immature avacados before the skin toughens. Soft skinned fruit such as guavas and mulberries are eaten voraciously by the birds.

In the aviary, White-eyes eat an even wider variety of food. Following Eddinger (1969), I fed mainly honeywater and high protein cereal as staples. Other food included apples, bananas, oranges, papaya, grapefruit, cantelope, mango, avacado, pineapple, mulberry, lettuce, figs, potatoes, rasins,peaches, pears, plums, guava, onions, fingerfruit, jelly, tangerines, syrup, bread, chocolate, cookies, hamburger, and a variety of insects.

In other parts of the world, Zosterops has been accused of spreading plants. In Australia, Gannon (1936) describes several species that had been carried to his yard by White-eyes and they included loquats, blackberries, lantana, asparagus, and mistletoe. The spread of lantana in Hawaii has been attributed to the Mynah (Caum, 1933), but it appears that the White-eye may have played a part also.

Table 11

Food Eaten by White-eyes (1972-1973)

Common Name	Scientific Name
Fruit	
Octopus tree	Brassaia actinophylla
Red Pepper	Capsicum frutescens
Fiddlewood	Citharexylum spinosum
Tangerines	Citrus nobilis
Autograph tree	Clusia rosea
Java Plum	Eugenia cumini
Surinam Cherry	Eugenia uniflora
Banyan	Ficus lacor
Banyan	Ficus retusa
Fern tree	Filicium decipiens
Litchi	Litchi chinensis
Mango	Mangifera indica
White Mulberry	Morus alba
Mock Orange	Murraya exotica
Avacado	Persea americana
Date Palm	Phoenix sp.
Allspice	Pimenta dioica
Strawberry Guava	Psidium cattlelanum
Guava	Psidium guajava
Christmas Berry tree	Schinus terebinthifolius
Nectar	
Pink Shower	Cassia grandis
Palm tree	Cocos sp.
Gold tree	Cybistax donnell-smithii

Table 11 (cont.)

Common Name	Scientific Name
Nectar (cont.)	
Tiger Claw	*Erythrina variegata*
Silver Oak	*Grevillea robusta*
Hybiscus	*Hybiscus* sp.
Sausage tree	*Kigelia pinnata*
---------	*Norantoa guianensis*
African Tulip	*Spathodea campanulata*
Pink Tecoma	*Tabebuia* sp.

Why has the species been so successful in Hawaii?

From its introduction in 1929 to present, the White-eye has become the most abundant bird in Hawaii, more successful in numbers than the other exotics and endemics. By studying the reproductive biology and natural history, several reasons for this become apparent.

When first introduced here, the high breeding success and low mortality, rapid growth of the young (more broods per season for each pair), and rapid sexual maturity, enabled the birds to build up a sizable breeding population quickly. After the rapid establishment, the species was able to spread and invade new areas by means of winter flocking. White-eyes do well in a variety of habitats. They are now found in the very wet and dry areas of the islands, at all elevations.

The birds readily nest in a wide variety of trees and eat an equally wide variety of fruits, nectars, and insects. Exotic and endemic trees and plants in Hawaii are utilized by the birds. With the decrease in native plants in Hawaii, expecially in the lowlands, the birds would not be adversely affected. Furthermore, members of Zosterops characteristically do well in disturbed areas. And the territorial behavior of the species allows an efficient utilization of the available vegetation and area. This helps to maintain a high breeding population.

Wind and rain are the most important environmental factors in Hawaii, during the breeding season. White-eyes seem to have special behavior patterns in nest site selection that helps to minimize these effects. Furthermore, nesting occurs during an optimim period of the year.

The birds are sedentary, of advantage to an island population. There is no annual migration that could carry large numbers of them off the islands. Instead individuals remain in one area to reproduce year after year. A few juveniles are integrated into the population each season, maintaining the population.

Predators that were present in Japan may be absent here in Hawaii, and this could contribute to a much higher success rate here. And with the decrease of native birds, whether or not White-eyes were a factor in their reduction, there might be many empty niches available. Being generalists, the White-eyes would be able to fill some of the vacancies.

Many of the above mentioned reasons for the success of the birds in Hawaii is characteristic of *Zosterops* in general. The birds were in many ways 'preadapted' for island life before being brought here. As mentioned in the introduction, birds in this family have colonized more oceanic islands than any other family. In light of all this, the phenomenal success of the species in Hawaii is not unexpected.

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